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# The Effects of Fire on Forest Community Composition, Structure, and Pattern in Florida Sandhills.

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# THE EFFECTS OF FIRE ON FOREST COMMUNITY COMPOSITION, STRUCTURE, AND PATTERN IN FLORIDA SANDHILLS

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Botany

by
Alan John Rebertus
B.S., University of Minnesota, 1980
M.S., Louisiana State University, 1982
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ABSTRACT

The influence of fire on turkey oak (Quercus laevis Walt.) and sand live oak (Q. geminata Small) populations was examined in experimental fires in sandhills near Tampa. Turkey oak crown survival was positively related to oak dbh, distance to the nearest longleaf pine (Pinus palustris Mill.), and dbh of the nearest pine. The pyrogenic litter of pines adversely affected survival of small turkey oaks within 10-20 m of the nearest pine, depending on fire severity. Resprouting of crown-killed turkey oaks was inversely related to oak dbh and, in one field, distance to the nearest pine. Poor resprouting away from pines was associated with delayed crown mortality and incomplete release from apical dominance.

Turkey oaks were weakly clumped to randomly distributed at most scales in unburned fields. Four-year changes in a plot unburned for >21-25 yr suggested that as stands mature, trees become more randomly distributed. Initial fires reduced turkey oak densities by 41-57% and (1) reduced the scale of maximal clumping, (2) increased clumping intensity, and (3) created large-scale randomness and uniformity. Patchiness of surviving trees was probably related to spatial variation in fire intensity, particularly with distance from pines. Repeated fires increased clumping intensity and gradually eroded large-scale randomness and

uniformity, with most trees surviving only in a few isolated patches.

Mainly small sand live oaks (<10 cm dbh) were killed by initial fires, and subsequently larger trees were lost only very slowly from repeated annual and biennial fires. Although fuel characteristics within sand live oak groves display fire-retarding characteristics, fire mortality was mainly dependent on the size of individual trees, and not with grove size or location of trees within a grove. Trees suffered high crown mortality from intense fires occurring near longleaf pines, although mortality rates tapered off rapidly beyond the perimeter of the pine's crown. Age-class structures of groves recovering from fire suggested that even-aged cohorts of resprouts develop after some fires, but new sprouts are also produced annually as part of normal clonal growth and expansion. Sand live oaks are well adapted to sandhill as well as less frequently burned scrub and hammock communities.

# INTRODUCTION

Sandhills were formed from Pleistocene marine deposits found along the coastal plain from Alabama to North Carolina (Laessle 1958). The vegetation of frequently-burned xeric sandhills in central Florida is savanna-like, dominated by scattered longleaf pines (Pinus palustris Mill.), turkey oaks (Quercus laevis Walt.), sand live oaks (Q. geminata Small), and wiregrass (Aristida stricta Michaux) groundcover (Williamson and Black 1981). Frequent thunderstorms in early summer are responsible for lightning-caused fires, which prior to settlement probably burned sandhills every 3-4 yr (Chapman 1932, Christensen 1981).

The effects of fire on vegetation in the Southeast are the most striking in North America (Garren 1943), yet successional relationships in sandhills are still poorly understood. Sandhills are often closely associated with sand pine (Pinus clausa (Chapm. ex Engelm.) Vasey ex Sarg.) scrub; and although the two communities are sometimes separated only by a narrow ecotone, scrub burns only once every 20-50 yr (Richardson 1977). Kurz (1942) believed that sandhill is succeeded by scrub, and others have noted that scrub species sometimes invade sandhills in the absence of fire (Laessle 1958, Snedaker 1963, Veno 1976, Myers 1985, Myers and White 1987). Miller (1950), however, suggested that scrub can develop into sandhills; while Laessle (1958)

doubted whether there was any successional relationship between sandhills and scrub. Myers (1985) hypothesized that sandhills may become scrub and vice versa, depending on fire history. Allelopathic shrubs may influence the fire frequency in scrub by inhibiting the growth of wiregrass (Richardson and Williamson (in press)).

The invasion of unburned sandhills by mesic hardwoods led many researchers to believe that sandhills will succeed to mesic hammock forest in the continued absence of fire (Monk 1960, Snedaker 1963, Veno 1976). Christensen (1981), however, suggested that long-term fire exclusion was not characteristic of sandhills, and invasion by hardwoods was evidence of "stagnation," rather than continued succession. Abrahamson (1984) and Givens et al. (1984) also believed that succession (in the Clementsian sense) was not occurring in unburned southern-ridge sandhills.

Regardless of successional trends, longleaf pine, turkey oak, and sand live oak are all very tolerant of frequent sandhill fires. The fire adaptations of longleaf pine, in particular, have been well studied. Fire is required for successful seed germination, seedling release, and control of disease and competing hardwoods (Mattoon 1922, Siggers 1932, Heyward 1939, Gemmer et al. 1940, Wahlenberg 1946). Williamson and Black (1981) suggested that longleaf pine's needle litter could be an adaptive trait, facilitating intense fire in the vicinity of pines.

They found that turkey oaks were more likely to suffer fire mortality under longleaf pines than out in the open. Williamson and Black (1981) also reported that surface fire temperatures were relatively mild in the sand live oak groves, which seem to retard fire.

Are pyrogenic and apyrogenic traits adaptive? If so, how is the fitness of a plant possessing the trait enhanced? Part I and Part II of this study take a closer look at longleaf pine pyrogenicity from the perspective of turkey oak crown survival, resprouting, and spatial pattern. Part III examines the effects of fire on sand live oak crown survival, resprouting, and spatial pattern - with special reference to possible benefits of grove formation. The objectives of this study were:

(1) To examine the factors affecting turkey oak and sand live oak survival after experimental sandhill fires and develop models describing these relationships.

(2) To develop simulation models projecting changes in sandhill oak populations with repeated fires.

(3) To better understand the life history of sandhill oak species, their response to fire, and their relationship to long-term successional changes in sandhill and adjoining scrub and hammock communities.

Of the estimated 24 million ha of longleaf pine forests present in colonial times, less than 25% now remain (Croker and Boyer 1975). Most existing tracts are highly degraded from logging and changes in fire regime, such as the longleaf pine-dominated sandhill community in Florida, which is now considered endangered (Means and Grow 1985). At present, turkey oaks dominate most sandhills, even in preserves where frequent winter fires have been reintroduced (Myers and White 1987). A better understanding of the role of fire in sandhills is paramount to the successful restoration and management of this rapidly disappearing community.

# I. LONGLEAF PINE PYROGENICITY AND TURKEY OAK MORTALITY

# INTRODUCTION

The dominant trees in sandhills of the Southeastern Coastal Plain have unique life history attributes for thriving in well-drained sands and surviving surface fires which may have been as frequent as every 3-4 yr prior to settlement (Chapman 1932, Heyward 1939). Longleaf pine is the most fire-tolerant southern pine (Heyward 1939), and its well-aerated, highly combustible needle litter is considered pyrogenic or fire-facilitating (sensu Mutch 1970), generating very intense fires in the vicinity of pines (Williamson and Black 1981, Platt et al. 1988).

Although the evolutionary mechanism for selection of pyrogenic traits has been questioned (Snyder 1984), fire most likely increases the fitness of longleaf pines by enhancing seed germination and seedling survival. Fire plays an important role in (1) preparing a mineral-soil seedbed which promotes germination (Buttrick 1914, Wahlenberg 1935, Chapman 1936, Osborne and Harper 1937, Gemmer et al. 1940, Bruce and Bickford 1950, Bruce 1951), (2) controlling brown-spot disease (Scirrhia acicola) (Siggers 1932; Wahlenberg 1935; Bruce 1951, 1954; Maple 1977; Grelen 1978), and (3) reducing competition from grasses and hardwoods (Mattoon 1922; Pessin 1933, 1938; Chapman 1926, 1932, 1936; Pessin and Chapman 1944; Wahlenberg 1946; Bruce and Bickford 1950; Smith 1955; Grelen

1978; Williamson and Black 1981). Increased flammability can influence directly the edaphic and biotic factors critical to germination and seedling survival of longleaf pines, or their fitness may be indirectly enhanced if the pines are released from competitors damaged by the fire (Buckley 1984). On xeric sites, longleaf pine seedlings encounter serious competition from turkey oaks, which are notoriously resistant to fire (Heyward 1939). Adult turkey oaks tolerate mild surface fires, and although smaller oaks are prone to crown mortality, they resprout vigorously (Heyward 1939, McGinty and Christy 1977, Williamson and Black 1981). Williamson and Black (1981) discovered that turkey oaks were more likely to suffer crown mortality from fire if they were located directly under the canopy of a longleaf pine than in the open. Although this relationship has been quantified to some degree, a more detailed study is needed to assess the full impact of longleaf pines on turkey oak crown survival as well as their resprouting. If longleaf pines enhanced the survival of their own seedlings by "repelling" turkey oaks and reducing competition, a possible mechanism favoring pyrogenicity could be proposed. However, if the effects of longleaf pine pyrogenicity on turkey oak crown survival are minimal and resprouting rates are high, then the interspecific competition hypothesis may be less likely.

Seventy-five percent of the original 24 million ha of

longleaf pine-dominated vegetation of the Southeast Coastal Plain has been eliminated, and most of the remaining pinelands are highly degraded due to man's exploitation and changes in the fire regime (Croker and Boyer 1975, Myers and White 1987). Longleaf pine-dominated sandhills in Florida are now considered an endangered community (Means and Grow 1985). Turkey oaks dominate most sandhills in peninsular Florida, even in preserves where frequent winter fires have been reintroduced (Myers and White 1987). Careful experimentation under relatively natural conditions will hopefully yield information to aid in the restoration and proper management of sandhills.

Experimental fires with pre- and post-fire sampling provided a data base for constructing multivariate models of turkey oak crown survival and resprouting ability. The objectives of this study were (1) to determine the magnitude of pyrogenic effects on turkey oak crown survival and resprouting ability, (2) develop a model to simulate the effects of repeated burning on turkey oaks, and (3) indirectly assess whether pyrogenicity reduces competition between pines and oaks.

## METHODS

### Experimental plots

Data for turkey oak crown survival and resprouting ability were collected from two experimental fires on the

200-ha University of South Florida Ecological Study Area, Tampa. Experimental fire plots cover 12 ha of sandhill dominated by longleaf pine and turkey oak, with sand live oak and bluejack oak (Q. incana Bartr.) subdominant. Saw palmetto (Serenoa repens Small) clumps are abundant in the understory, and wiregrass forms a dense groundcover. Mesic hardwood forest, bald cypress (Taxodium distichum L.) swamp, and scattered areas of sand pine scrub adjoin the sandhill. Sandhill geologic origin and soils are described by Laessle (1958).

Two recently unburned fields with 30-60 large longleaf pines/ha were chosen for this study to examine the initial, and presumably most dramatic, effects of pyrogenicity on turkey oaks. Fire histories of both fields were known, and they were unburned long enough for substantial regrowth of turkey oaks.

On 6 June 1981, a relatively mild experimental fire burned the 0.70-ha field 1. All woody vegetation $\geq$2.5 cm dbh (diameter breast height) was mapped in a 0.43-ha section of the field prior to the burn (February 1981), 9 mo after the fire, and 3.75 yr after the fire to account for delayed mortality. Crown-killed turkey oaks were examined for the presence of basal sprouts.

The second experimental fire, conducted on 27 May 1983 in the 0.50-ha field 2, was more intense. Previous burns in 1968, 1971, and 1974 had reduced turkey oak tree densities,

but the 9-yr fire-free period allowed many turkey oak resprouts to reach 3-5 cm dbh. A 0.39-ha plot in this field was mapped in spring, 1985, 1.9 yr after the last fire to determine post-fire vegetation. Although post-fire sampling was done earlier than in the other field, 1.9 yr presumably accounts for most delayed mortality. Dead aerial stems were also mapped to reconstruct pre-fire (1983) vegetation. Most of the dead stems were still standing, but some fallen trees were also mapped from stump remains. The dbh of dead trees was measured directly or estimated if some of the bark was missing. For trees still alive in 1985, their 1983 dbh was estimated from growth curves based on other burned fields in the study area.

Although field 1 had not been burned in at least 21 yr, the fire was relatively mild because the older turkey oak stands suppressed wiregrass growth, and the hardwood leaf litter was relatively inflammable (see Streng and Harcombe 1982). In contrast, the intense fire in field 2 was fueled by heavy wiregrass accumulations in the young, fairly open turkey oak stands. Also, the fire in field 1 was preceded by several days of precipitation, whereas the fire in field 2 was not. Turkey oaks suffered higher crown mortality in field 2 than in field 1 for the 2.5-5.5-cm dbh class (60% vs. 51%) and 5.5-10.5-cm dbh class (30% vs. 24%), but there was no difference in mortality for the $\geq$10.5-cm dbh class (17%) (see also Table 1, Fig. 1). The effects of fire on

field 2 were particularly noticeable since most of the trees were <5.0 cm dbh.

Finally, a 24-ha plot in a 0.81-ha "reference" field, unburned at least since 1960, was mapped in 1981 and again in 1985.

These and other fields in the study area are permanently marked, and trees have been numbered and tagged. Mapped data are archived at Louisiana State University and available to interested readers.

Statistical analysis

Logistic multiple regression (Walker and Duncan 1967) was used to model turkey oak crown survival and resprouting for the 2 burned fields and reference. The SAS LOGIST procedure (Harrell 1983) fits the logistic multiple regression model to a single binary (0-1) dependent variable; for example, "0" for "crown-dead" and "1" for "crown alive." The assumption of the model is:

the probability that the ith observation is 1 is:

$$P(Y_i=1|X_{i1}, X_{i2},\ldots, X_{ip}) = 1/[1 + e^{(-\alpha - \sum_{j=1}^{p}\beta_j X_{ij})}],$$

where $\alpha$ is the intercept, and the $\beta_j$ are the parameters associated with the p predictors. The following predictor variables were evaluated:

(1) turkey oak stem diameter (dbh)

(2) distances to the three nearest large ($\geq$ 10 cm dbh) longleaf pines

(3) diameters of the three nearest large ($\geq$ 10 cm dbh) longleaf pines.

Stepwise and backward elimination techniques were used to select statistically significant predictors based on maximum likelihood ratios. Colinearity between variables was low.

Several indices were used to assess the quality and predictive ability of the logistic regression models: (1) fraction of concordant pairs, (2) Somers' $D_{yx}$, (3) a classification table, and (4) an R statistic (see Harrell 1983). The first 3 indices were used to compare predicted probabilities generated from the model with the observed response. Concordance is the fraction of pairs in which the "live" observation has a higher predicted probability than the "dead" observation, computed from all possible "live-dead" (or "resprouted-not resprouted") pairs. Somers' $D_{yx}$ is an index of rank correlation between the predicted probabilities and the observed response, and the classification table was used to compare the actual number of live and dead trees with the predicted number, based on model probabilities. The R statistic for logistic multiple regression is similar to the multiple correlation coefficient and can be used to assess the predictive ability of the overall model, or, from the partial R's, the contribution of individual variables. Significant variables

were added until there was little change in R, concordance, Somers' $D_{yx}$, and the percent of observations correctly classified; and the values were generally substantially greater than for a model with only the intercept entered.

Fire simulation model

The logistic equations for crown survival and resprouting were combined with a growth equation and used to simulate the effect of 30 annual burns on an unburned field. An annual burn frequency was chosen because other complicating factors (seedling recruitment, sprout release, etc.) would not have to be taken into account. The main intent was to show how fast turkey oaks decline and the importance of resprouting. This model could also be used to predict changes in a turkey oak population subjected to fires every 2-3 yr, but recruitment from seedlings and resprouts becomes increasingly important for fires at longer intervals. The initial pre-burn status used in the simulation was based on actual densities and locations of trees and sprouts in field 1, which had been unburned in 1981 for at least 21 yr. A linear regression equation for growth (change in dbh vs. dbh) was generated from 2-yr dbh changes in an annually-burned plot (years 6-8 of the rotation). Trees experiencing crown death in the model were moved into the sprout class at the predicted rate. Subsequently, the sprout class was reduced 5% with each

fire, an estimate based on limited data from several plots, including an annually-burned field. Recruitment from seedlings and resprouts was assumed to be negligible with annual burning. Lack of recruitment is supported by data from frequently burned plots in the study area and also from observations of nearby rangeland burned at 1-2-yr intervals.

## RESULTS

### Crown survival

Turkey oaks in field 1 experienced only 25.9% crown mortality (119 of 458) 9 mo after a relatively mild fire, but delayed mortality raised the toll to 39.1% (179 of 458), 3.75 yr post-fire (Table 1). In field 2, the hotter burn resulted in 55.6% (278 of 500) crown mortality 1.9 yr after the fire. The pre- and post-fire size-class distributions indicate disproportionately high fire mortality for smaller trees (<5.5 cm dbh) with negligible differences for larger size classes in both burns (Fig. 1).

In field 1 the best model of crown survival (in terms of predictability and interpretability) included turkey oak dbh ("tDBH"), distance to the nearest longleaf pine ("DIST"), and dbh of the nearest pine ("pDBH") (Tables 2A and 3A):

$$Y = 1/[1 + e^{(0.706 - 0.240*tDBH - 0.107*DIST + 0.032*pDBH)}],$$

Table 1. Sandhill stand characteristics in experimental plots. Densities include recruitment. Longleaf pine basal area includes trees ≥2.5 cm dbh.

| | | Turkey oaks | | | | Longleaf pines | | |
|---|---|---|---|---|---|---|---|---|
| Field | Last fire (yr) | trees/ha >2.5 cm dbh | Avg. dbh (cm ± SD) | % of crown-killed trees resprouting | Basal area ($m^2$/ha) | trees/ha >10 cm dbh | Avg. dbh (cm ± SD) | Basal area ($m^2$/ha) |
| Field 1 | >21 | 1054 | 5.9 ± 5.0 | --- | 5.12 | 60 | 28.2 ± 10.0 | 4.28 |
| | 0.7 | 780 | 6.5 ± 5.6 | 91.6 | 4.71 | 60 | 28.2 ± 10.0 | 4.28 |
| | 3.75 | 642 | 7.2 ± 5.4 | 67.6 | 4.04 | 62 | 29.4 ± 10.2 | 4.76 |
| Field 2 | | | | | | | | |
| | 9 | 1279 | 4.2 ± 2.8 | --- | 2.50 | 28 | --- | --- |
| | 1.9 | 573 | 5.0 ± 3.4 | 94.6 | 1.66 | 28 | 30.1 ± 9.5 | 2.24 |
| Reference | | | | | | | | |
| | >21 | 1167 | 6.7 ± 4.0 | --- | 5.56 | 54 | 20.7 ± 8.5 | 2.31 |
| | >25 | 1042 | 6.9 ± 3.9 | 31.6 | 5.15 | 79 | 20.5 ± 8.3 | 3.12 |

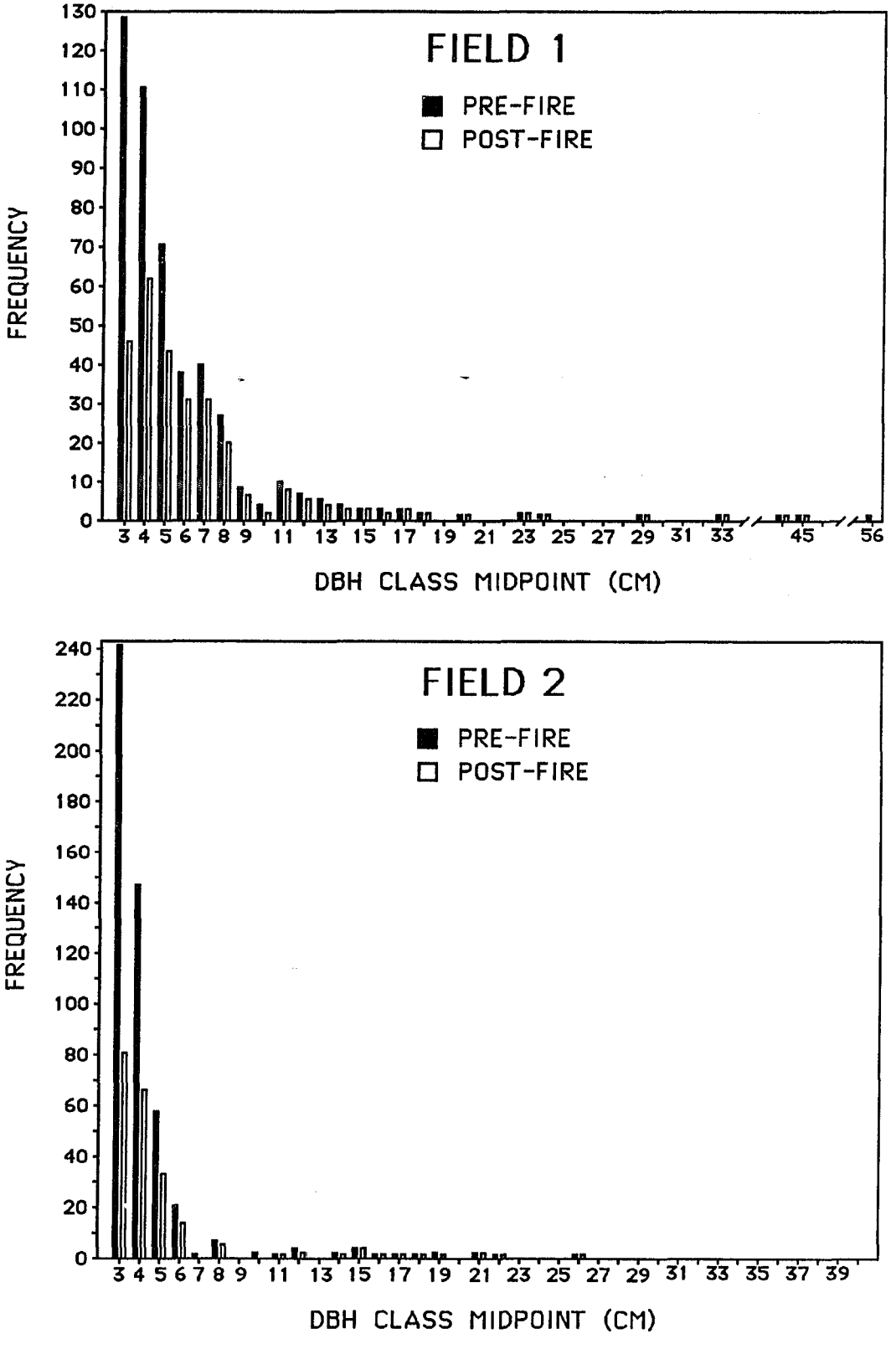



Figure 1. Pre- and post-fire dbh frequency distributions for turkey oaks (dbh at time of fire given).

Table 2. Statistical evaluation of logistic regression models of turkey oak crown survival (A), and resprouting ability (B) in fields 1 and 2. Indices of model predictive ability (see METHODS) are given, and values in parentheses are for models with only the intercept entered. Level of significance is indicated by "**" ($P \leq 0.01$).

A. Crown survival

| Model indices | Field 1 | Field 2 |
|---|---|---|
| -2 log likelihood statistic | 72.63 ** (3 df) | 137.88 ** (3 df) |
| Concordance | 0.76 (0.50) | 0.80 (0.50) |
| Somers' $D_{yx}$ | 0.52 (0.00) | 0.61 (0.00) |
| % correct classification | 70.7 (60.9) | 71.4 (55.6) |
| R | 0.33 (0.00) | 0.44 (0.00) |

B. Resprouting ability

| Model indices | Field 1 | Field 2 |
|---|---|---|
| -2 log likelihood statistic | 31.65 ** (2 df) | 30.30 ** (1 df) |
| Concordance | 0.74 (0.50) | 0.86 (0.50) |
| Somers' $D_{yx}$ | 0.49 (0.00) | 0.73 (0.00) |
| % correct classification | 73.2 (67.6) | 95.7 (94.6) |
| R | 0.35 (0.00) | 0.49 (0.00) |

Table 3. Statistical evaluation of logistic regression parameter estimates of crown survival (A), and resprouting ability (B) in fields 1 and 2 ("tDBH" = turkey oak dbh (cm), "DIST" = distance to the nearest large longleaf pine (m), "pDBH" = dbh of the nearest large longleaf pine (cm)). Chi-square statistics are with 1 df, and levels of significance are indicated by "*" ($P \leq 0.05$) and "**" ($P \leq 0.01$).

A. Crown survival

| | Field 1 | | | | Field 2 | | | |
|---|---|---|---|---|---|---|---|---|
| Variable | Beta | Std. error | Chi-square (1 df) | R | Beta | Std. error | Chi-square (1 df) | R |
| Intercept | -0.706 | 0.484 | 2.13 | --- | -1.791 | 0.431 | 17.24 ** | --- |
| tDBH | 0.240 | 0.045 | 28.86 ** | 0.21 | 0.333 | 0.075 | 19.29 ** | 0.16 |
| DIST | 0.107 | 0.038 | 14.08 ** | 0.14 | 0.118 | 0.014 | 72.29 ** | 0.32 |
| pDBH | -0.032 | 0.013 | 5.92 * | -0.08 | -0.041 | 0.010 | 16.80 ** | -0.15 |

B. Resprouting ability

| | Field 1 | | | | Field 2 | | | |
|---|---|---|---|---|---|---|---|---|
| Variable | Beta | Std. error | Chi-square (1 df) | R | Beta | Std. error | Chi-square (1 df) | R |
| Intercept | 3.565 | 0.634 | 31.61 ** | --- | 5.756 | 0.790 | 53.11 ** | --- |
| tDBH | -0.418 | 0.107 | 15.22 ** | -0.24 | -0.683 | 0.165 | 17.17 ** | -0.36 |
| DIST | -0.156 | 0.049 | 10.15 ** | -0.19 | --- | --- | --- | --- |

where "Y" is the probability of crown survival. The distances to the two nearest longleaf pines, as separate variables or added together, also worked equally well in the model, but the partial R's indicated that these variables accounted for little additional variation in the model. The distance to the nearest pine was chosen for simplicity and to conform with the significant variable "pDBH."

Crown survival was positively related to turkey oak stem diameter and distance to nearest longleaf pine (Fig. 2), and inversely related to the dbh of the nearest pine. The crown survival of smaller turkey oaks was particularly sensitive to the proximity of pines, with turkey oaks in the 2.5-cm dbh class influenced up to at least 10 m. Beyond 10 m the confidence limits become too wide for interpretation.

In field 2 the best model of crown survival again included turkey oak dbh, distance to the nearest longleaf pine, and dbh of the nearest pine (Tables 2A and 3A):

$$Y = 1/[1 + e^{(1.791 - 0.118*DIST - 0.333*tDBH + 0.041*pDBH)}].$$

The distances of the two nearest pines, separately or added together, as well as the distances of the three nearest pines added together, all worked about equally well in the model. The partial R's indicated that these variables accounted for very little additional variation, and the overall model was not significantly improved, so the

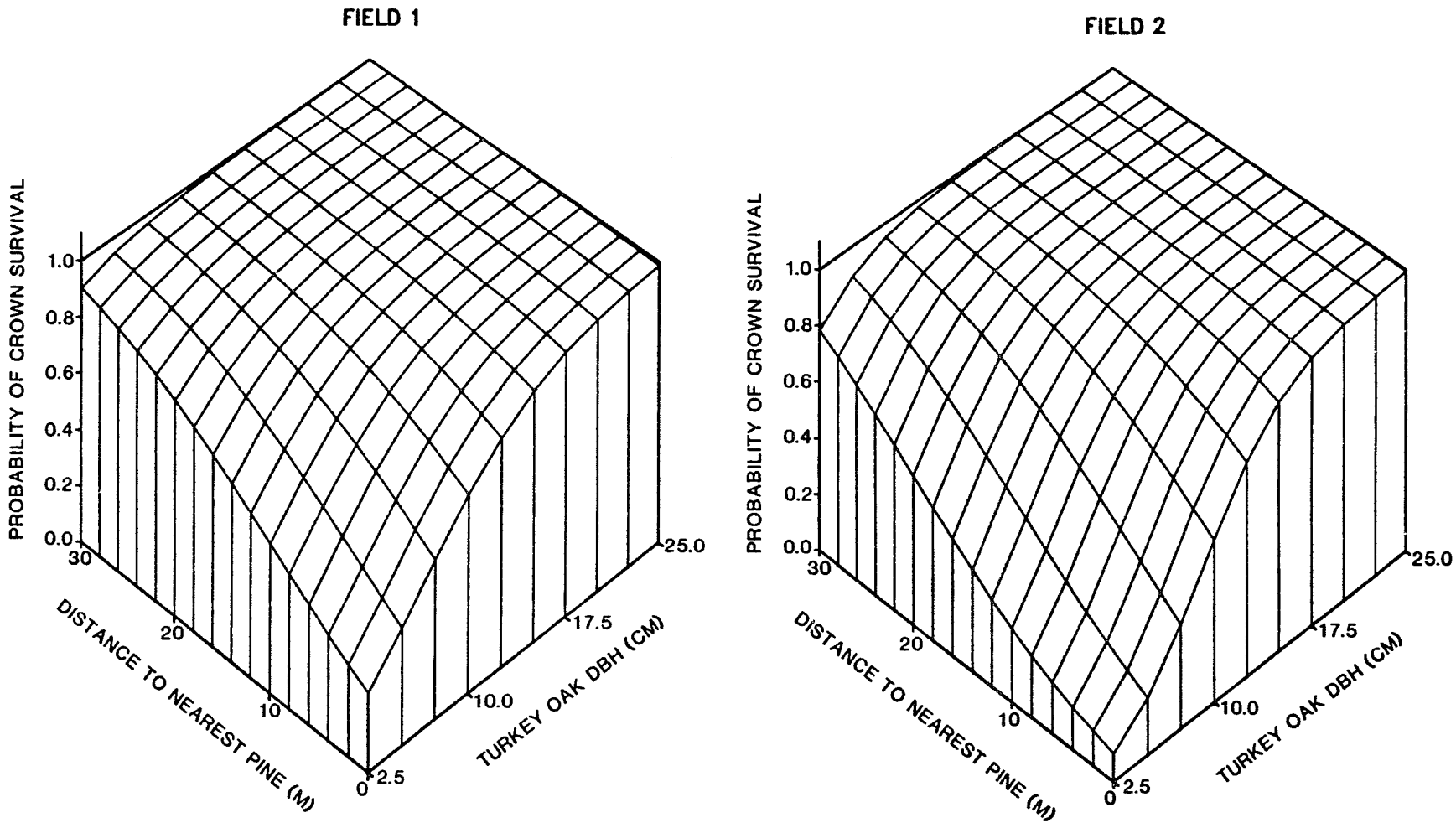



Figure 2. Logistic models for turkey oak crown survival in a mild burn (field 1) and a hotter fire (field 2). Mean longleaf pine dbh's were used for computing probabilities of crown survival. The maximum oak-to-nearest-pine distance for field 1 is 19 m, but the range of the model has been extended for comparison to field 2.

distance to the nearest pine was chosen for simplicity.

As in the milder burn, crown survival was positively related to turkey oak stem diameter and distance to the nearest pine (Fig. 2), and inversely related to the dbh of the nearest pine. However, the distance to the nearest pine was more important than turkey oak dbh in the model for the hotter fire (Table 3A). Crown survival rates were similar to those in field 1, except that smaller turkey oaks were more vulnerable overall, and vulnerable at greater distances from the nearest pine. Pines appeared to influence 2.5-cm dbh turkey oaks out to 25-30 m, although mortality was fairly low at these distances. A zone of nearly 100% turkey oak crown mortality appeared to extend 5-15 m around most of the larger pines in the field.

In the unburned reference field, there was 13.6% mortality (38 of 280) in the 3.75 yr between samples. Neither turkey oak dbh, the distance to the nearest pine, nor the dbh of the nearest pine was significant ($P>0.05$) in the logistic model of crown survival for the reference field.

Resprouting ability

Nine months after the fire in field 1, 91.6% of the crown-killed turkey oaks (109 of 119) had resprouted. By 3.75 yr post-fire, only 67.6% of the crown killed turkey oaks (121 of 179) had resprouts. Twenty trees which

initially resprouted following crown death had their resprouts die by 3.75 yr post-fire. The main reason for the decline in resprouting, however, was the poor resprouting rate for oaks with delayed mortality. Of the 60 trees experiencing delayed mortality (between 9 mo and 3.75 yr post-fire) only 53.3% resprouted. Forty-four of the 60 trees (73.3%) had resprouts from the base while they were still living 9 months after the fire, but only 28 of these were successful resprouters 3.75 yr after the fire. Only 4 trees with live crowns and lacking resprouts at 9 mo post-fire, later developed resprouts following crown death.

The best logistic model of resprouting ability in field 1 included turkey oak dbh ("tDBH"), and the distance to the nearest pine ("DIST") (Tables 2B and 3B):

$$Y = 1/[1 + e^{(-3.565 + 0.418*tDBH + 0.156*DIST)}],$$

where "Y" is the probability of a crown-killed turkey oak resprouting. Resprouting ability was positively related to the dbh of the nearest pine ($P \leq 0.05$), but this variable was not included in the model because of the poor residual chi-square to degrees of freedom ratio (Harrell 1983), and lack of improvement in the overall model.

Resprouting ability of crown-killed oaks was inversely related to both turkey oak dbh and the distance to the nearest pine (Fig. 3). Small oaks located near pines had

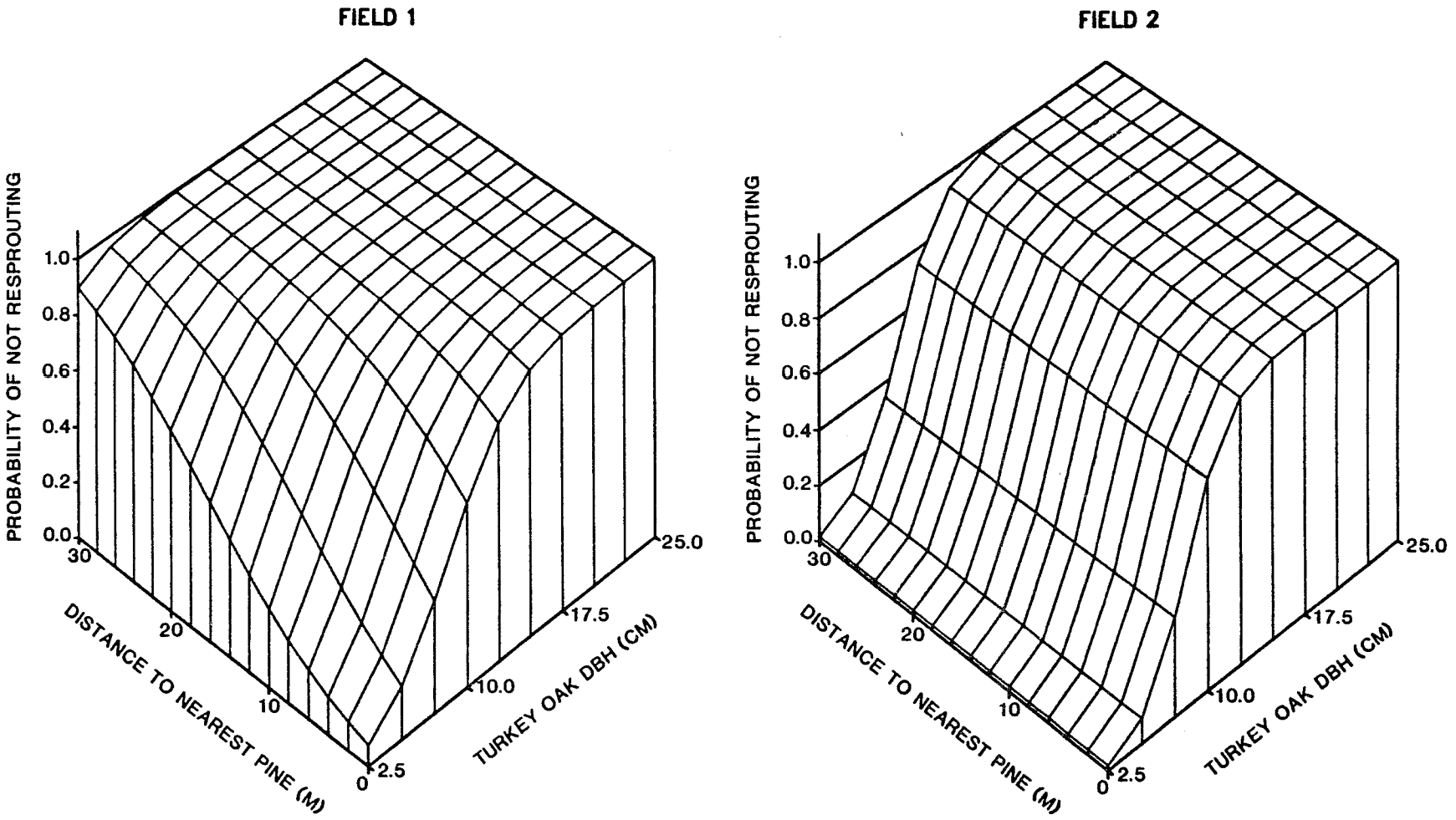



Figure 3. Logistic models for turkey oak resprouting ability in a mild burn (field 1) and hotter fire (field 2). The probability of not resprouting (1-Y) is plotted to expose the entire response surface. In field 2, the nonsignificant "distance to nearest pine" variable was assumed to have a slope of "zero."

the highest resprouting rates, almost 100%, but resprouting declined to less than 50% for trees further than 16 m from a pine. Larger oaks rarely resprouted, regardless of location. In field 2 the resprouting rate 1.9 yr after the fire was still 94.6% (263 of 278). Presumably, delayed mortality >2 yr only slightly reduces the resprouting rate. The only significant variable in the logistic model was turkey oak dbh (Tables 2B and 3B):

$$Y = 1/[1 + e^{(-5.756 + 0.683*tDBH)}].$$

Resprouting ability was inversely related to turkey oak dbh (Fig. 3), but only 15 trees failed to resprout.

In the reference field, only 31.6% (12/38) of the crown-killed turkey oaks resprouted, and none of the model variables was significant.

## DISCUSSION

Williamson and Black (1981) found that turkey oaks were more likely to suffer crown mortality during a fire if they were located directly beneath a pine, where fires were more intense, than out in the open. Results from both burns support their finding, and indicate that pines influence the survival of smaller turkey oaks well beyond the perimeter of their crowns (ca. 4 m radius). Despite different stand

structure and fire intensity between the two fields, the resulting pattern of crown mortality was quite similar. In the hotter fire, smaller turkey oaks (<5 cm dbh) were more vulnerable and pines appeared to influence their survival at greater distances than in the mild burn. For larger oaks, there was little difference in crown mortality between fields. Due to the greater relative abundance of small turkey oaks in the second field, the fire drastically changed the vegetation, but the effect on a tree of given size and location was, nevertheless, very similar in both fires.

In the milder burn, crown-killed turkey oaks appeared to form discrete clusters around the larger pines, perhaps extending 4-5 m beyond their crown perimeters; in contrast, crown mortality in the hotter fire was not confined to discrete clusters around individual pines but was more generalized around the entire pine grove. Smaller turkey oaks appeared to be affected by pines 25-30 m away. In both fields, the distance to the second nearest pine was significant in the logistic model, and in field 2 the sum of the three nearest pines added together was significant. This could indicate a "grove effect" influencing turkey oak crown survival, but more likely it is an artifact of the pine's natural clumping, since the second and third nearest pines explained very little additional variation in the model. For turkey oaks more isolated from pines, the

influence of the nearest pine may be negligible or blurred by the collective effect of several pines.

Most of the needle litter accumulates directly beneath a pine's canopy, and needles also lodge in the foliage of turkey oaks, making them extremely vulnerable near pines. Although the accumulation of needle fuel beyond the pine's crown is negligible, the convective heat of the flame front moving through a pine grove may generate considerable downwind fire intensity and kill more turkey oaks than would be predicted by fuel content alone.

It is well known that fire tolerance in hardwoods increases with stem diameter (McCarthy and Sims 1935; Heyward 1939; Harrington and Stephenson 1955; Ferguson 1957, 1961; Williamson and Black 1981). Fire resistance tends to increase as trees become larger, the bark thickens, and crowns grow above the level of surface fires (McCarthy and Sims 1935).

The inverse relationship between resprouting and stem diameter is also fairly well documented for hardwoods subjected to crown damage or death from fire and such forestry practices as cutting, girdling, and poisoning (Bull and Chapman 1935, Heyward 1939, Keetch 1944, Williston 1949, Ferguson 1957, Woods and Cassady 1961). Heyward (1939) found that fires frequently killed older "scrub oaks" (including turkey oaks) >19 cm dbh, but only increased the density of stems in younger age classes.

The increased resprouting with proximity to longleaf pines is more difficult to explain. The higher probability of resprouting near pines is not simply an artifact of smaller turkey oaks being more abundant near pines, since the relationship holds within dbh classes. Because trees with delayed crown mortality were largely responsible for the poor resprouting response, perhaps the nature of fire damage plays some role. A quick, thorough destruction of the crown would immediately remove the crown's apical dominance, allowing the tree to resprout with full use of the underground carbohydrate reserves. However, if only the lower stem has been girdled, apical dominance may continue to suppress resprouting, and carbohydrate reserves may be used in the maintenance of a dying crown (Bull and Chapman 1935, Woods 1955). Many fire-damaged oaks resprouted within 9 mo, suggesting that the crown's apical dominance had been partially removed. Of those trees later experiencing crown death, however, nearly 40% had their resprouts die within 3 yr, suggesting that a slow crown death may have hindered resprout survival. Thus, it appears that mild fires may be more effective in killing turkey oaks, although hot fires result in more crown mortality. A review of both fires (Table 1) shows crown mortality of 39% in field 1 and 56% in field 2, but tree mortality of 13% in field 1 and 3% in field 2. Crown mortality was sensitive to the proximity of pines in both fires, whereas tree mortality was sensitive to

the proximity of pines only in the mild fire.

By plotting the probability of turkey oak survival (either with an intact crown or by resprouting), some indication of the size and locations favorable to turkey oaks is apparent (Fig. 4). Large turkey oaks isolated from pines will almost always survive a fire with an intact crown. And even though small turkey oaks located near pines are prone to crown death, they are also virtually invulnerable to fire because of their extremely high resprouting rate (>95%). In field 2 the trees with lowest probability of survival are in the 8-11-cm dbh range, because they are neither vigorous resprouters nor immune from crown mortality. In field 1, intermediate-sized trees located near pines also have relatively low survival. These trees are not quite large enough to be immune from crown mortality, especially close to a pine, but they also are too large to resprout exceptionally well. The survival minimum tends to shift away from pines for the smaller turkey oaks. Surprisingly, oaks in the 2.5-3.5-cm dbh range have lowest survival far from pines because they are still prone to crown mortality, but resprouting rates are not exceptionally high. Mild surface fires would probably girdle many of the smallest trees, and thus suppress resprouting. Although resprouting allows turkey oaks to persist near pines, clearly oaks located further from pines will have higher crown survival, mast production (if they are large enough),

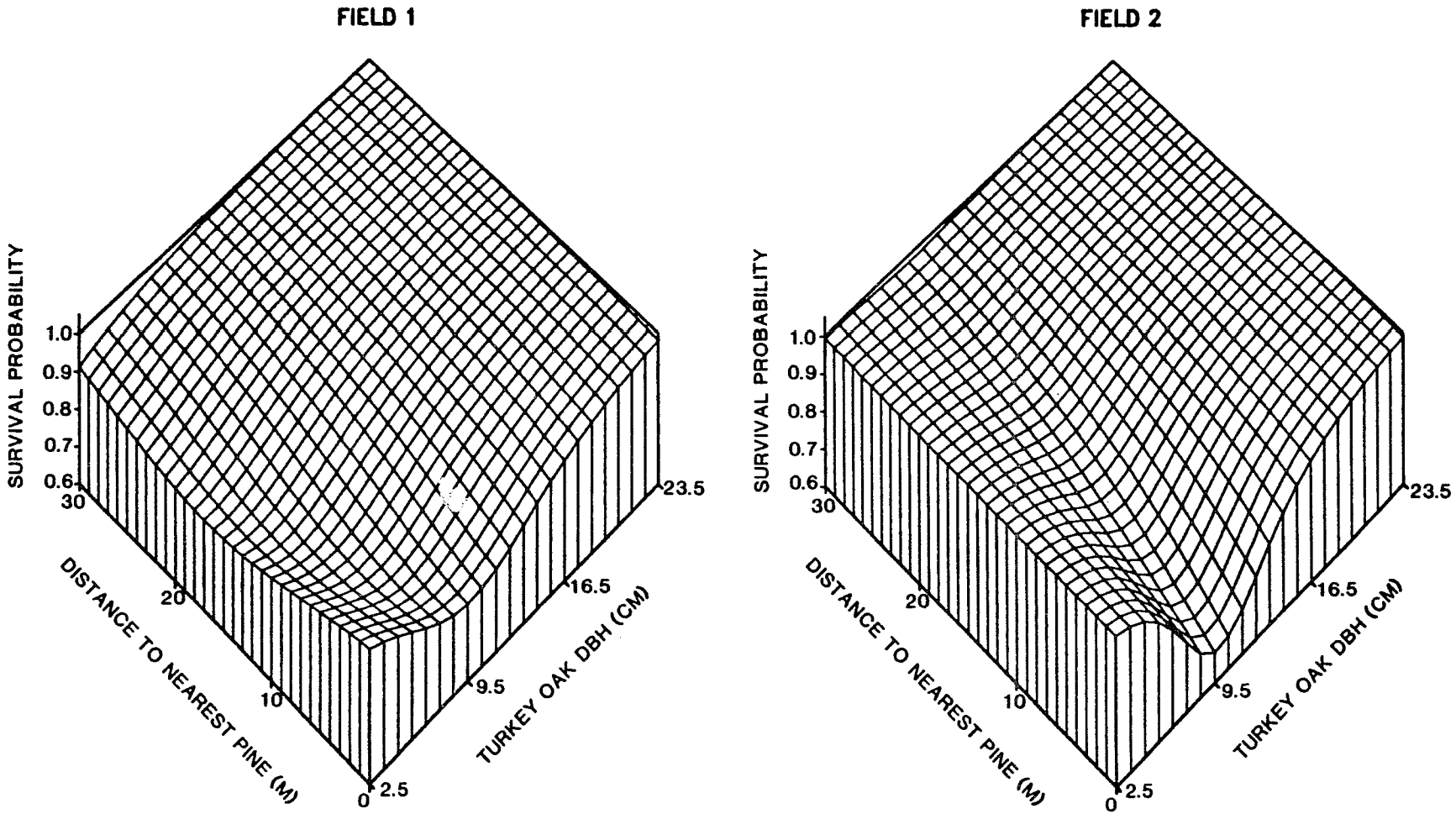
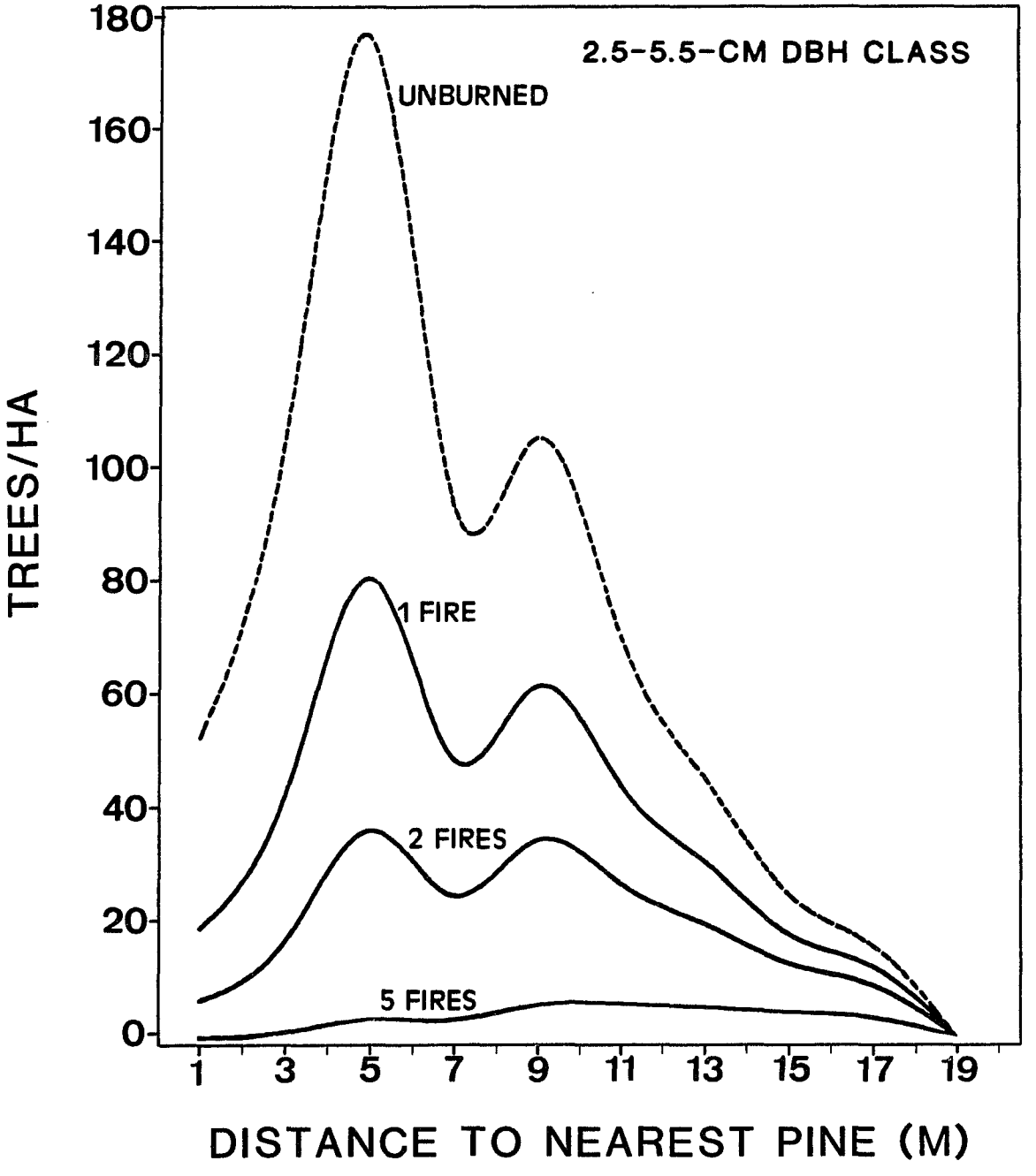


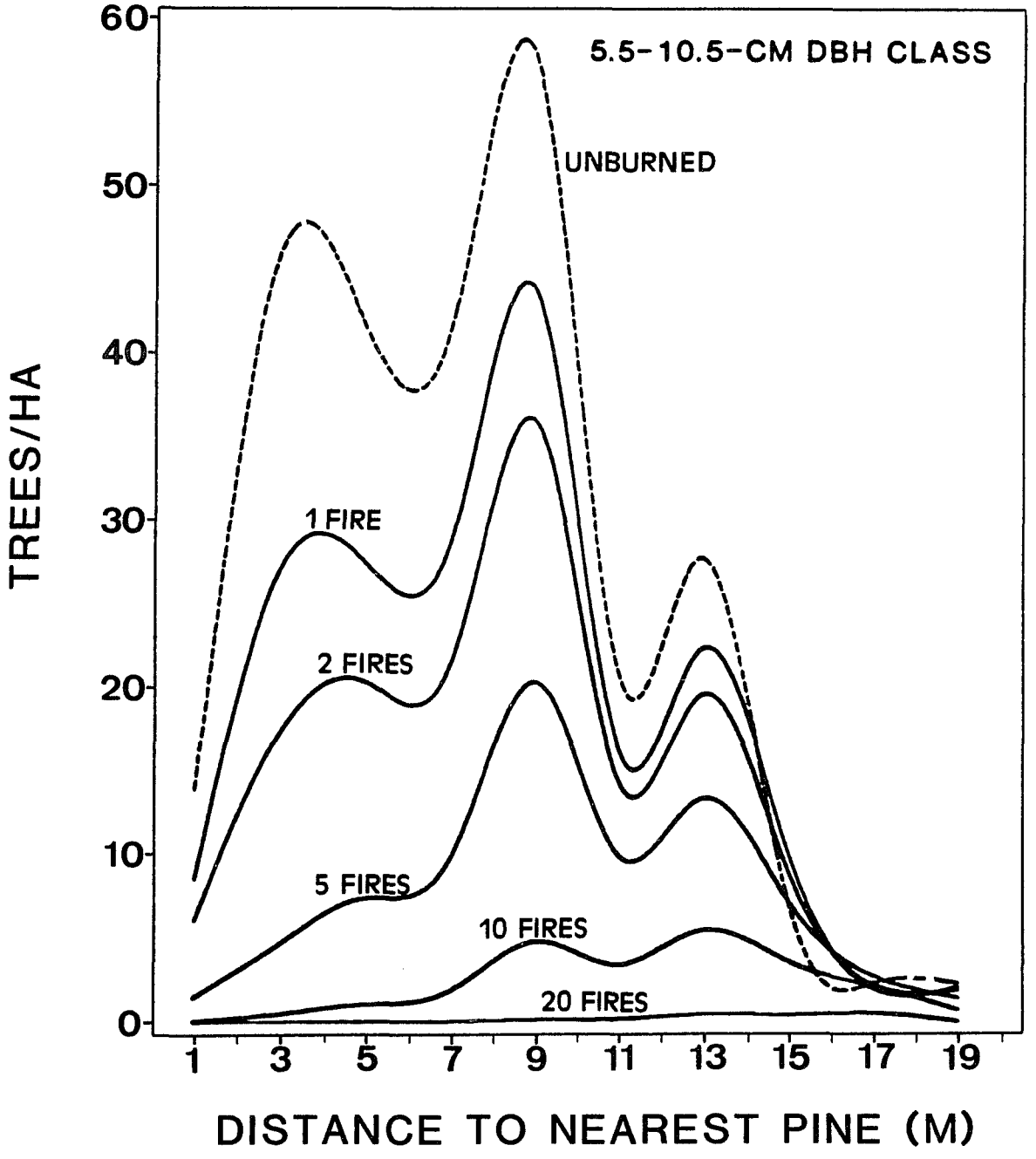

Figure 4. Probability of turkey oak survival (with intact crown or by resprouting following crown death) in a mild fire (field 1) and hotter fire (field 2). Values generated by adding predicted probabilities for crown survival and resprouting (corrected for total number of trees).

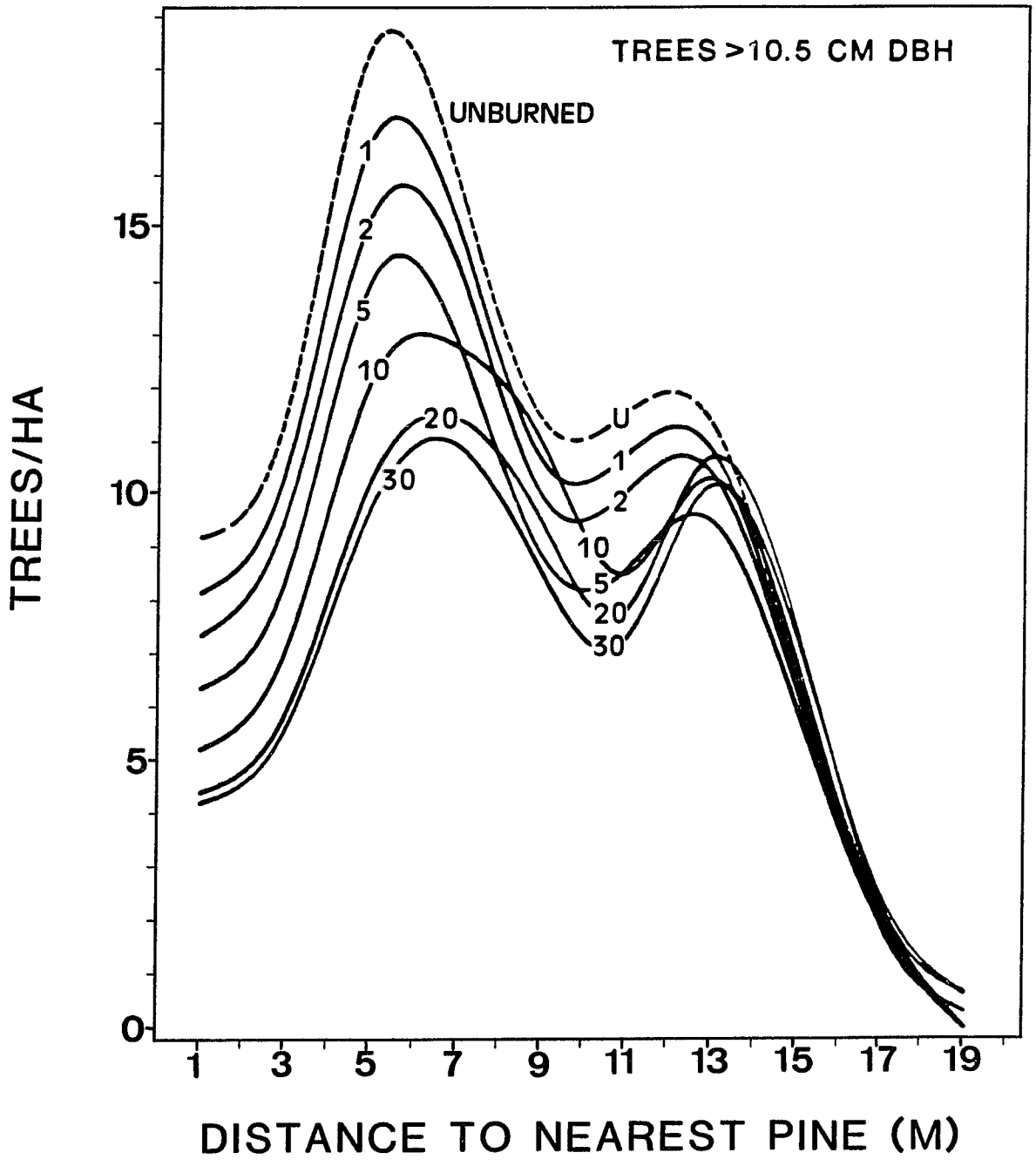
and higher fitness as long as the sprouts are suppressed by repeated fires.

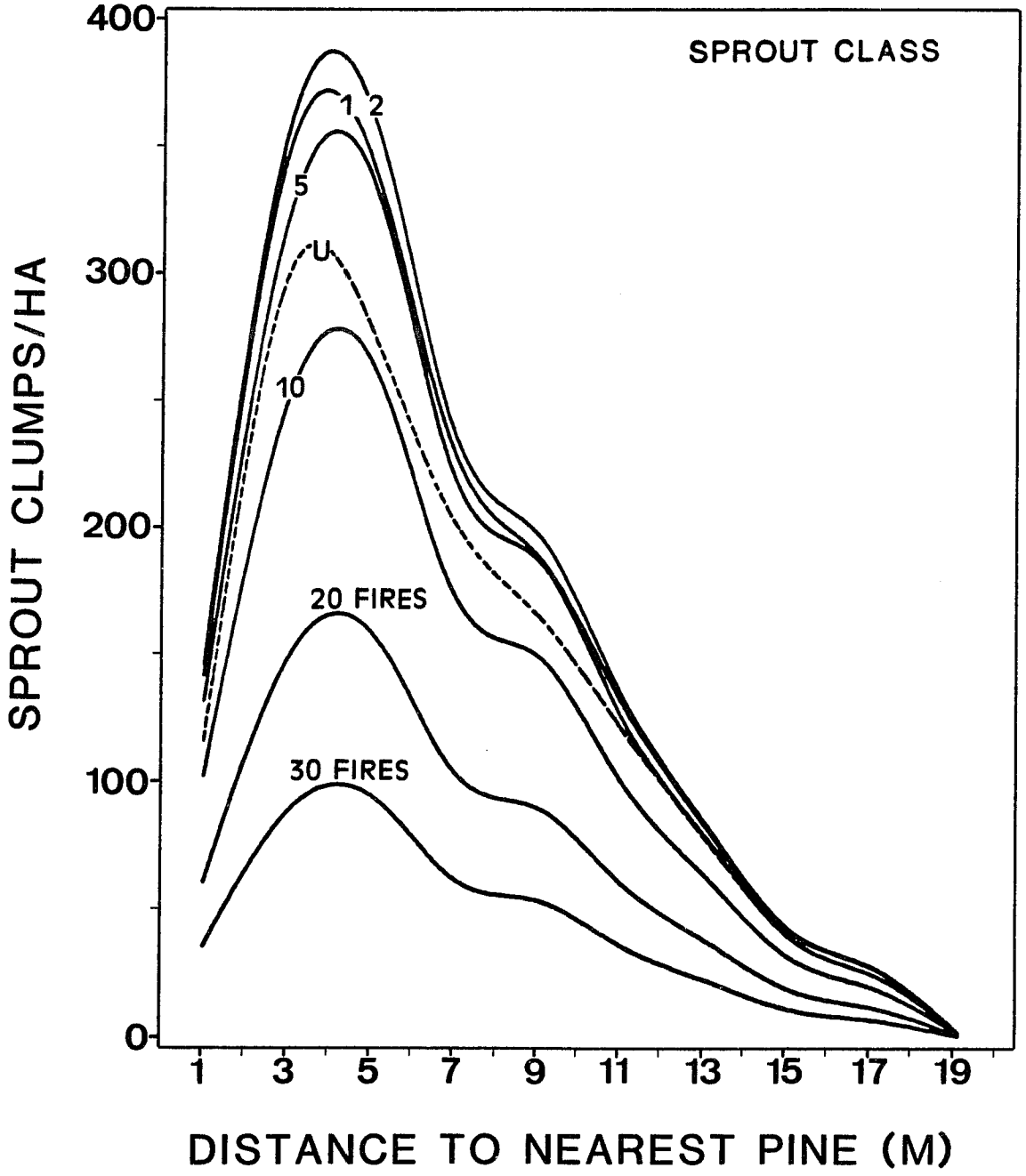
The simulation model for 30 annual burns predicts that turkey oaks in the 2.5-5.5-cm dbh class will decline rapidly with the first 2-3 fires, especially near pines (Fig. 5). After 10 fires, all trees in this class will have died, resprouted, or grown into the next dbh class. The median distance to the nearest pine for a turkey oak in the 2.5-5.5-cm class increases from 6.2 m in the unburned state to 7.5 m after 1 burn and 10.9 m after 5 fires. Trees in the 5.5-10.5-cm class decline most rapidly during the first few burns, but a few trees remain far from pines after 20 fires. The median distance from the nearest pine increases from 7.4 m in the unburned state to 8.1 m after 1 fire, and to 12.0 m after 10 fires. Besides higher crown mortality for trees located closer to pines, there is slight recruitment from the 2.5-5.5-cm class between the first and tenth fire at 14-16 m from a pine, which also accounts for the increase in median distance. For the largest turkey oaks (>10.5 cm dbh), there is a steady decline in abundance over time at distances less than 7 m from a pine. After 10 burns, however, recruitment outweighs crown mortality at distances greater than 7 m from a pine. At 9 m, the density almost reaches pre-burn levels. Recruitment is minimal between 9-12 meters due to the paucity of trees at this distance in the 5.5-10.5-cm class, but recruitment beyond 14

Figure 5. Simulated turkey oak densities with annual burning. Dashed line (--U--) is the unburned status of a hypothetical population (based on field 1 in 1981), and other curves depict tree densities after the indicated number of fires. Model assumptions are given in the METHODS section.


2.5-5.5-CM DBH CLASS
UNBURNED
1 FIRE
2 FIRES
5 FIRES
TREES/HA
180
160
140
120
100
80
60
40
20
0
1
3
5
7
9
11
13
15
17
19
DISTANCE TO NEAREST PINE (M)


5.5-10.5-CM DBH CLASS
UNBURNED
1 FIRE
2 FIRES
5 FIRES
10 FIRES
20 FIRES
TREES/HA
0
10
20
30
40
50
60
1
3
5
7
9
11
13
15
17
19
DISTANCE TO NEAREST PINE (M)


TREES >10.5 CM DBH
UNBURNED
1
2
5
10
20
30
U
1
2
10
5
20
30
TREES/HA
0
5
10
15
1
3
5
7
9
11
13
15
17
19
DISTANCE TO NEAREST PINE (M)


SPROUT CLASS
1
2
5
U
10
20 FIRES
30 FIRES
SPROUT CLUMPS/HA
400
300
200
100
0
1
3
5
7
9
11
13
15
17
19
DISTANCE TO NEAREST PINE (M)

m brings the density above pre-burn levels. By the thirtieth fire, recruitment has shifted further away from pines. The median distance of the larger turkey oaks increases only slightly, from 7.3 m in the unburned state to 8.7 m after 30 fires.

Many crown-killed trees will resprout, and the model predicts that sprouts will increase for the first few years, reflecting the massive crown death of trees in the 2.5-5.5-cm class. With most of the smaller trees gone, new resprouts fail to balance the 5% annual sprout loss (see METHODS), and by the tenth fire sprout densities are lower than pre-burn levels. After 30 fires, the density is about 30% of the original density. No one has ever documented how long turkey oak sprouts can resprout before depleting their underground reserves. In fields unburned for more than 10 yr, sprouts typically have more than 85% of their biomass underground (unpublished data), suggesting that sprouts may easily recover from repeated top removal. Chattaway (1958) found that some eucalypts could withstand 27 consecutive defoliations and still regenerate. Despite higher resprouting rates for trees located near pines, the model predicts that the median distance from pines will decrease only slightly, from 5.8 m in the unburned state, to a minimum of 5.6 m after two fires, to 5.7 m after 30 fires. The sprouts shift closer to pines only with the first few fires, and the high pre-burn density of sprouts swamps the

effect of just a few fires. With annual burning, resprouts would continue resprouting at a high rate and probably never reach tree size. Sprouts would tend to shift closer to pines if fire intervals were longer and allowed sprouts to regrow into the canopy and face the greater probability of resprout failure away from pines. Malanson and Westman (1985) used a computer simulation of different fire regimes to show that shrub sprouting was potentially very important in determining long-term vegetation composition in California coastal sage scrub.

The original distributions of sprouts and small trees are skewed nearer to pines than the distribution of larger turkey oaks (Fig. 5). Even though the pre-burn data represent at least 21 fire-free years, apparently some sprouts have remained suppressed in the understory for many years, and others have periodically been released into the smaller tree class. The larger trees located further from the pines probably persisted through fires which crown-killed most trees close to pines and left the huge population of resprouts. Alternatively, it is possible that many turkey oaks have remained suppressed near the large pines due to competition for light or water, rather than as a response to fire.

Although the models in this study were generated from large data sets, more replication of experimental fires would be desirable. Furthermore, because crown

vulnerability and resprouting responses are likely to change with repeated fires (as fire damage mounts and fuel loads change) the models may not be useful for predicting exact densities after a given number of fires. Despite these limitations, other experimental plots in the study area tend to confirm some of the basic predictions of the simulation model: (1) most small trees die and resprout after just a few fires at relatively short intervals, and (2) larger trees tend to persist in pockets isolated from pines. Many large turkey oaks eventually have fallen during windstorms, and this type of death is apparently related to burn scars enlarged by repeated fires.

Pines clearly have a profound influence on turkey oak crown survival and resprouting, but does pyrogenicity increase the fitness of longleaf pine? Longleaf pine seedlings may also be killed by the intense fires near adult pines (Bruce 1951, Davis 1955, Boyer 1974, Platt et al. 1988), and the similar effects of intense fires on longleaf pine seedlings and turkey oak make selection for pyrogenicity in response to turkey oak competition questionable. Turkey oak mortality is still a function of distance from adult pines, however, and within areas of maximum pine regeneration, pyrogenicity probably reduces competition between pines and oaks. A few large, scattered, surviving turkey oaks may actually favor longleaf regeneration as well, by providing shade and moderating the

extremely xeric conditions of the deep sands (Gaines 1950; Allen 1954, 1956). Turkey oak sprouts may be more harmful to pine regeneration than large trees (Bull and Chapman 1935), so suppression of resprouts away from adult pines would also favor pines. Unfortunately, longleaf pine recruitment on the study plots was insufficient to test these hypotheses.

Under a natural fire regime, with fires every 3-4 yr, longleaf pine will suppress turkey oaks and its own fitness may be enhanced. However, under an irregular fire regime, pyrogenicity might actually increase the fitness of turkey oaks located near pines relative to other areas. Their persistence vegetatively near pines may insure future reproductive output during a period of infrequent fires. Thus, the question of the adaptive significance of pyrogenicity cannot be clearly resolved without considering the long-term effect of many fires on the survival and regeneration of longleaf pine and turkey oaks.

# II. FIRE INDUCED CHANGES IN TURKEY OAK SPATIAL PATTERN

# INTRODUCTION

Both physical and biotic components of the environment interact to create distinct spatial patterns within plant communities, which can be broadly classified as random, clumped, or regular. Clumped patterns are most frequently encountered in communities simply because suitable habitat tends to be patchy, or because reproduction (vegetative or by propagule) is usually concentrated around adult plants (Whitford 1949, Kershaw 1958, Greig-Smith and Chadwick 1965, Laessle 1965, Anderson 1967, West 1969, Hall 1970, Owen and Harberd 1970, Westman and Anderson 1970, Payandeh 1974, Bonnicksen 1975, Gill 1975, Williamson 1975, Hubbell 1979, and Whipple 1980). Random patterns are less common, but may arise when plants display (1) efficient seed dispersal, as in ponderosa pine (Pinus ponderosa) (Cooper 1961), (2) growth on very uniform sites (e.g. Salicornia; Ashby 1935, Brereton 1971), or (3) high tolerance of environmental conditions, as in the shade tolerance of sugar maple (Acer saccharum) and American beech (Fagus grandifolia) (Williamson 1975). Vegetation may approximate a random pattern as individuals in younger age classes (which tend to be clumped) are culled out, leaving adults more widely spaced (Yeaton 1978, Good and Whipple 1982). Eventually competition or other factors may lead to regular spacing, such as occurs in mature stands of ponderosa pine (Cooper

1961, West 1969), sand pine (Laessle 1965), Quercus spp. (Christensen 1977), white fir (Abies concolor) and sugar pine (Pinus lambertiana) (Bonnicksen 1975), and some bottomland hardwoods (Whipple 1980, Good and Whipple 1982).

Succession often has a profound effect on community composition and structure, and not surprisingly, pattern also changes (Whitford 1949; Greig-Smith 1952, 1961, 1964; Pielou 1966; Anderson 1967; Brereton 1971; Yarranton and Morrison 1974; Bonnicksen 1975; Christensen 1977). Most of these studies suggest that community pattern tends to progress from clumped to random to regular with succession. These changes are generally very gradual with long-term forest maturation and accompanying changes in species composition and structure. Disturbance starts the cycle over again, beginning with post-disturbance plants colonizing suitable patches.

A few studies have dealt with the effect of fire on pattern (Cooper 1961, Laessle 1965, West 1969, Bonnicksen 1975, Gill 1975). Fires that destroy existing vegetation often create favorable seedbeds for regeneration, resulting in a mosaic of even-aged stands (Cooper 1961, West 1969, Bonnicksen 1975). In communities where fire is not catastrophic (e.g. savannas), changes in pattern are liable to be more subtle.

Florida's xeric sandhills probably burned once every 3-4 yr prior to settlement (Chapman 1932, Christensen 1981),

and the dominant tree species, longleaf pine and turkey oak, are very resistant to mild surface fires (Heyward 1939, McGinty and Christy 1977, Platt et al. 1988). Longleaf pine seedlings survive frequent fires by remaining in an arrested "grass" stage for several years, during which the apical bud is protected. Grass-stage seedlings older than 4-5 yr are usually released by fire, and after a few years of rapid elongation, they may be tall enough to survive subsequent surface fires. Pines appear to be most susceptible to fire during the first 2 yr of the grass stage and again during the first several years of elongation. Crown-killed pines rarely resprout. Turkey oaks, in contrast, are vulnerable to crown mortality in all stages of early growth, but nevertheless recover through vigorous basal resprouting. Large turkey oaks have thick bark and tolerate mild surface fires.

I expected that turkey oak mortality in sandhill fires would be non-random, causing substantial changes in spatial pattern. First, smaller turkey oaks are more vulnerable to fire than larger turkey oaks. If, like most tree species, small turkey oaks are more clumped than the larger adults, then fire might result in a more random distribution of trees. Second, turkey oaks are more likely to suffer fire mortality in the vicinity of longleaf pines, where highly combustible needle litter generates locally intense fires (Williamson and Black 1981). Thus, variation in fire

intensity might lead to extreme patchiness in surviving trees. The purpose of this study was to examine how turkey oak pattern actually changed in experimental sandhill fires, and how differential mortality, as a function of size and proximity to pines, influenced pattern.

## METHODS

### Study area

All trees ≥2.5 cm dbh were mapped in plots in the 200-ha University of South Florida Ecological Study Area, Tampa, Florida. Experimental plots were established in sandhills dominated by longleaf pine and turkey oak, with sand live oak and bluejack oak subdominant. Saw palmetto, wiregrass, and turkey oak sprouts dominated the understory. Study fields ranged from 0.39-0.84 ha in size (Table 4), and with the exception of one January wildfire in the 5-year field (its first fire), all were burned with headfires in late May and early June.

Two fields were sampled before and after single fires: "initial-A" was unburned for 9 yr prior to the experimental fire, and "initial-B" was unburned for at least 21 yr prior to the burn. Prior to the 1983 experimental fire in the initial-A field, previous fires occurred in 1968, 1971, and 1974; however, extensive regrowth occurred during the 9-yr period. The initial-A field was mapped 2 yr after the 1983

fire, but pre-fire vegetation was reconstructed completely from dead stems. For trees surviving the fire, pre-fire (1983) dbh was estimated from linear regression growth equations based on data from other fields.

In addition to the single fires above, pattern data were collected from four other fields: (1) "1-year field" (8 annual fires), (2) "2-year field" (4 fires at 2-yr intervals), (3) "5-year field" (3 fires at 5-yr intervals), and (4) "reference field" (unburned for at least 21-25 yr). The reference field was mapped in 1981 and 1985. Turkey oaks were mapped after fires 4, 6, and 8 in the 1-year field; after fires 3 and 4 in the 2-year field; and after fires 2 and 3 in the 5-year field. In addition, vegetation prior to the earliest mapping was partially reconstructed from available dead stems in each field. The partial reconstruction probably included stems from the most recent fire prior to sampling, as well as some trees killed in earlier fires. Although vegetation in the 1, 2, and 5-year fields was not mapped prior to the first fires, aerial photographs and plot and transect data suggested that turkey oak densities were similar in all fields.

## Statistical analysis

Overall spatial pattern was tested using Donnelly's (1978) index based on nearest neighbor distances. Nearest neighbor, G(y), and point to nearest event, F(x), cumulative

distribution functions and Ripley's (1977) L(t) (square-root transformation of Ripley's K) were used to fully characterize pattern over a continuous scale (Diggle 1983, Moser 1987). G(y) and F(x) were generally not sensitive to changes in pattern in this study; thus, only L(t) will be presented. L(t) is based on the second moments of the spatial pattern (Ripley 1977) and uses all inter-tree distances: for example, if t=2, L is determined from the number of trees within 2 m of each tree, summed over all trees. Formulae for calculating these functions can be found in Ripley (1977), Diggle (1983), and Moser (1987). Monte Carlo tests were used to evaluate the statistical significance of the observed L(t) under the null hypothesis of complete spatial randomness. A 95% confidence envelope was created from high and low values of L(t) generated from 19 simulated random point distributions. All analyses were performed using the SAS macro SPATIAL (Moser 1987). Empirical functions were boundary-corrected and plotted at 1-m intervals. When sample sizes were adequate, separate analyses were performed on small (2.5-5.5 cm dbh), large ($\geq$5.5 cm dbh), and crown-killed trees ($\geq$2.5 cm dbh).

The pattern of turkey oak genets was analyzed in several unburned fields and the 1-year field after 8 fires. Genets included trees $\geq$2.5 cm dbh as well as smaller stems or clumps of stems isolated by at least 20 cm from other clumps or stems. Separate clumps were usually found to be

different individuals upon excavation, except for sprouts originating from opposite sides of large stumps.

Several ambiguous terms used in describing pattern are defined as follows. Clumping "intensity" refers to the magnitude of the deviation from randomness. "Scale" refers to pattern at a particular radius around each tree. For example: a pattern with maximum clumping at a scale of 7 m suggests clumps of 7-m radii. "Hierarchial" clumping over scales of 1-30 m means that small clumps of 1-m radii make up progressively larger clumps, up to 30-m radii.

## RESULTS

### Pattern in recently unburned fields

Turkey oaks in both unburned initial and reference fields were clumped overall, based on Donnelly's index and L(t) (Table 4, Figs. 6-8). Turkey oaks $\geq$2.5 cm dbh were clumped over the entire scale from 1-30 m (Figs. 6-8). In both initial fields, clumping intensity of trees $\geq$2.5 cm dbh and in the 2.5-5.5-cm dbh class increased progressively up to about 28 m (hierarchically clumped), whereas turkey oaks $\geq$2.5 cm dbh in the reference plot were maximally clumped at 10 m in 1981, and at 10-15 m in 1985. In both unburned initial and reference fields, small turkey oaks (2.5-5.5 cm dbh) were more clumped than large turkey oaks ($\geq$5.5 cm dbh), based on Donnelly's index and L(t).

Table 4. Plot data and overall spatial pattern of turkey oaks based on Donnelly's (1978) index. Mean nearest neighbor distance (NN), Donnelly's test statistic, and sample sizes are given ("**" = significantly clumped at P≤0.01; "*" = significantly clumped at P≤0.05; "ns" = not significantly different than random, P>0.05).

| | Number | Last | Plot | Large | Donnelly's Index - Turkey oaks | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | >2.5 cm dbh | | | 2.5-5.5 cm dbh | | | >5.5 cm dbh | | | Dead >2.5 cm dbh | | |
| Field | of fires | fire (yrs.) | area (ha) | pines /ha | NN (m) | index | (n) | NN (m) | index | (n) | NN (m) | index | (n) | NN (m) | index | (n) |
| Initial-A | 0 | 9 | 0.34 | 29 | 1.20 | -4.50 ** | (470) | 1.27 | -4.70 ** | (420) | 4.03 | -0.99 ns | (50) | --- | --- | --- |
| | 1 | 1.9 | 0.34 | 29 | 1.67 | -5.42 ** | (200) | 1.74 | -6.07 ** | (162) | 4.97 | -0.22 ns | (38) | 1.38 | -7.14 ** | (270) |
| Initial-B | 0 | >21 | 0.43 | 60 | 1.35 | -6.36 ** | (431) | 1.65 | -5.28 ** | (281) | 2.39 | -3.04 ** | (150) | --- | --- | --- |
| | 1 | 3.75 | 0.43 | 62 | 1.81 | -4.30 ** | (252) | 2.60 | -3.02 ** | (118) | 2.75 | -1.35 ns | (134) | 2.02 | -5.01 ** | (179) |
| 1-year pre | 4 | --- | 0.18 | 11 | 1.99 | -2.19 * | (94) | --- | --- | (24) | --- | --- | (70) | --- | --- | --- |
| | 6 | 0.9 | 0.18 | 6 | 2.63 | -1.61 ns | (56) | --- | --- | (15) | --- | --- | (41) | --- | --- | --- |
| | 8 | 0.7 | 0.18 | 6 | 2.78 | -1.76 * | (48) | --- | --- | (12) | --- | --- | (36) | --- | --- | --- |
| 2-year pre | 3 | --- | 0.37 | 38 | 2.95 | -3.10 ** | (76) | --- | --- | (24) | --- | --- | (52) | --- | --- | --- |
| | 3 | 1.7 | 0.37 | 38 | 3.51 | -3.38 ** | (44) | --- | --- | (9) | --- | --- | (35) | --- | --- | --- |
| | 4 | 0.7 | 0.37 | 38 | 4.19 | -2.59 ** | (35) | --- | --- | (9) | --- | --- | (26) | --- | --- | --- |
| 5-year pre | 2 | --- | 0.37 | 73 | 1.87 | -5.69 ** | (157) | --- | --- | (70) | --- | --- | (87) | --- | --- | --- |
| | 2 | 3.75 | 0.37 | 67 | 2.79 | -2.46 ** | (95) | --- | --- | (35) | --- | --- | (60) | --- | --- | --- |
| | 3 | 0.7 | 0.37 | 60 | 5.20 | -1.86 ** | (25) | --- | --- | (2) | --- | --- | (23) | --- | --- | --- |
| Reference | 0 | >21 | 0.17 | 76 | 1.35 | -3.70 ** | (178) | 1.84 | -2.77 ** | (94) | 1.96 | -2.61 ** | (84) | --- | --- | --- |
| | 0 | >25 | 0.17 | 112 | 1.40 | -3.66 ** | (161) | 1.80 | -4.02 ** | (80) | 1.93 | -3.06 ** | (81) | --- | --- | --- |

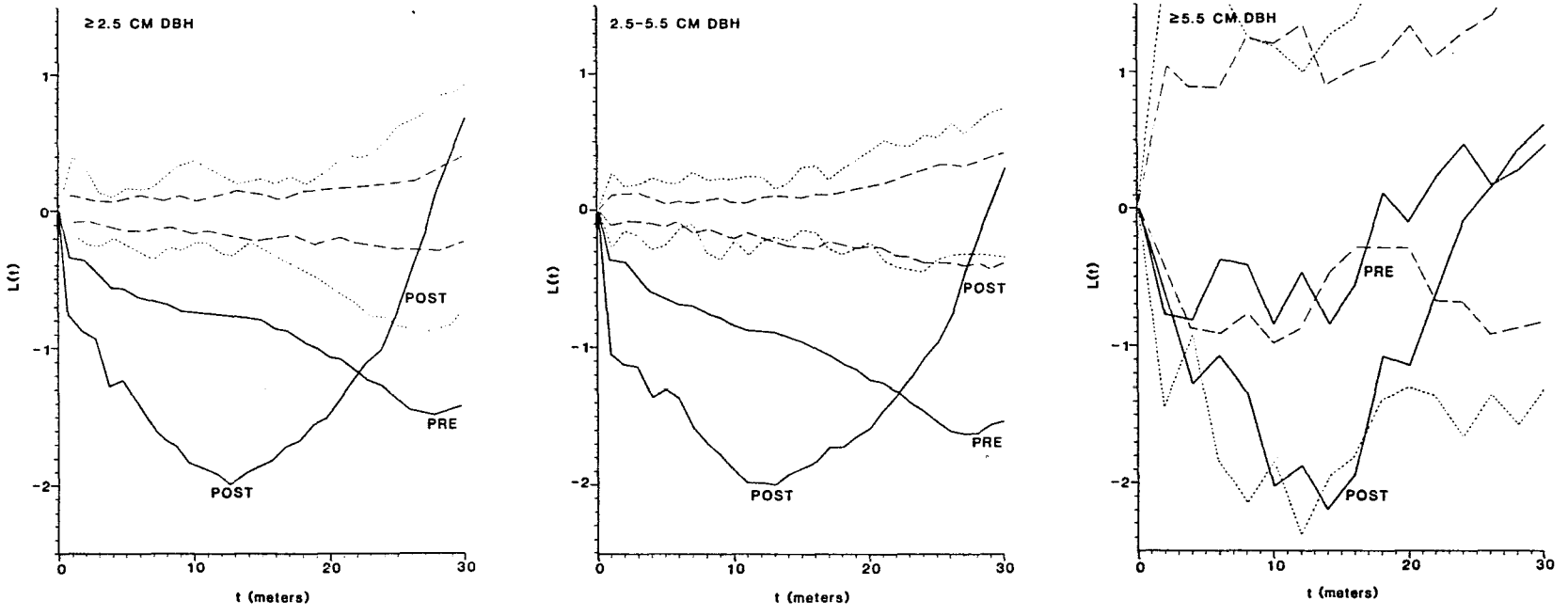



Figure 6. Ripley's L(t) plots for turkey oaks in initial-A field (9 yr unburned, then burned once). Pre and post-fire empirical functions and their respective Monte Carlo simulation envelopes have been overlaid for comparison. If the observed function falls below its envelope, the pattern is clumped ($P \leq 0.05$); if the observed function lies within its envelope, the pattern is random ($P > 0.05$); and if the function rises above the envelope, the pattern is uniform ($P \leq 0.05$). If pre- and post-fire simulation envelopes are highly overlapped, changes in L(t) can be interpreted directly; however, if the envelopes differ substantially, changes in L(t) must be interpreted with respect to the position of the envelopes.

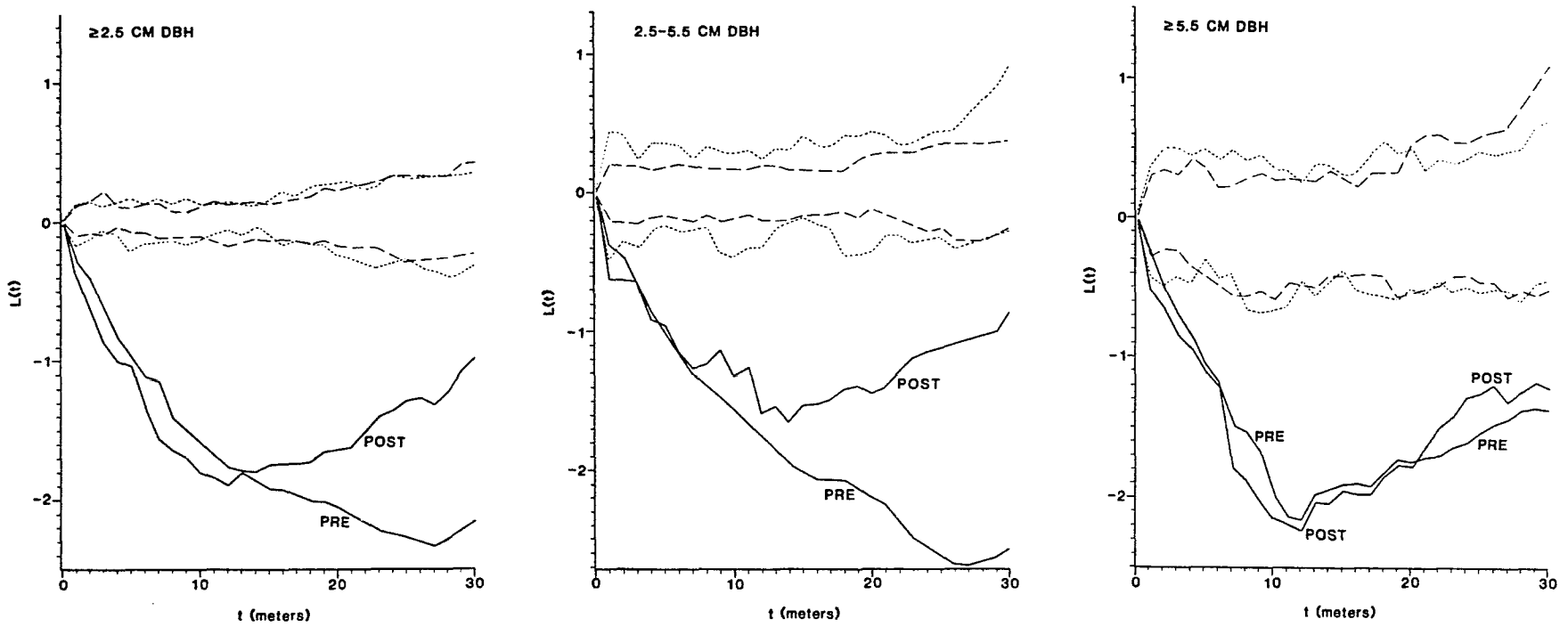



Figure 7. Ripley's L(t) plots for turkey oaks in initial-B field (21 yr unburned, then burned once) (see Fig. 6 for further explanation).

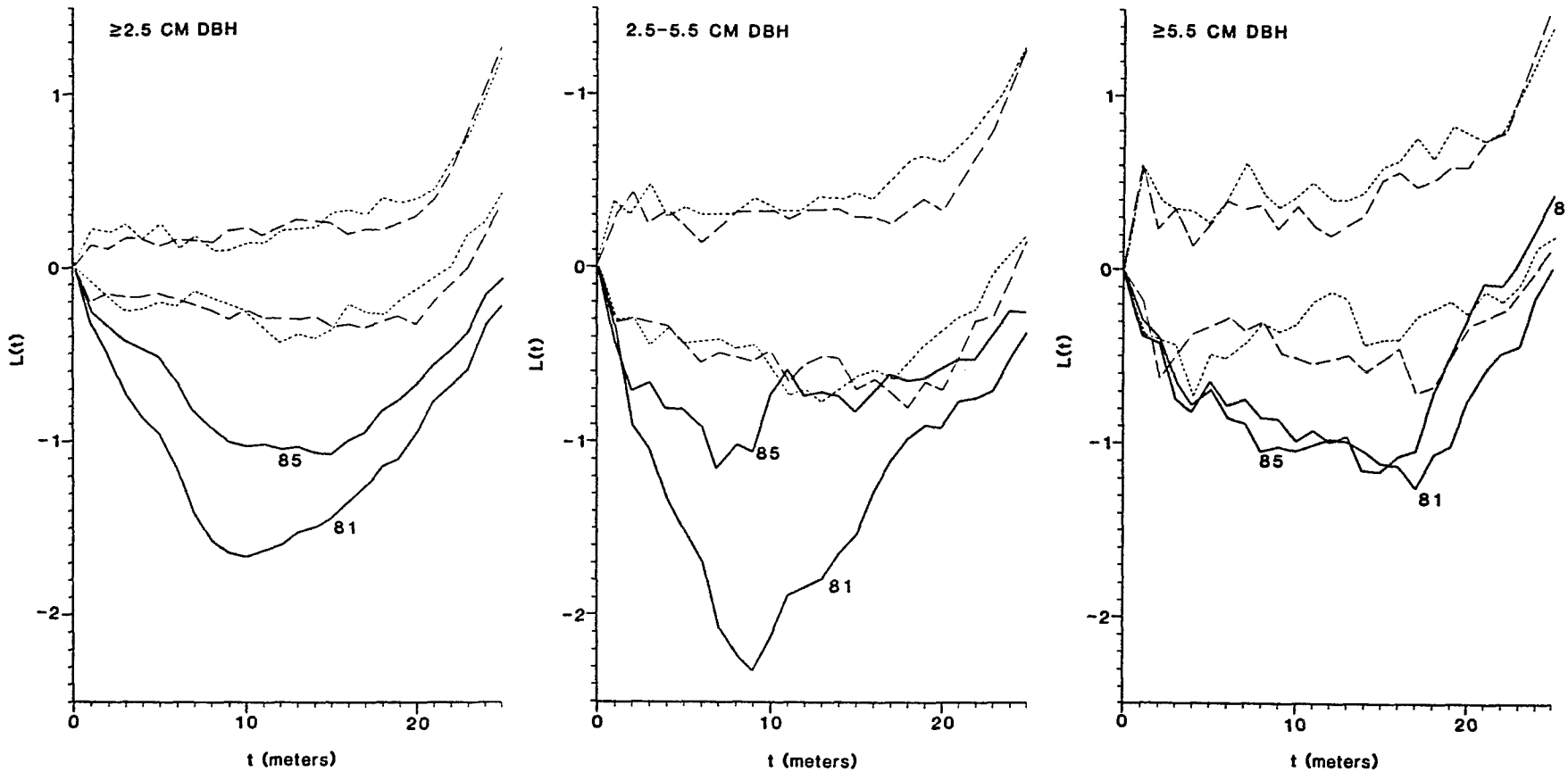



Figure 8. Ripley's L(t) plots for turkey oaks in the reference field. 1981 (unburned 21 yr) and 1985 (unburned 25 yr) empirical functions and their respective Monte Carlo simulation envelopes have been overlaid for comparison (see Fig. 6 for further explanation)

Although the number of turkey oaks in the reference plot declined by only 10% from 1981-1985, 27 trees died and 10 were recruited so the population was actually more dynamic. Eight additional recruits near the plot boundary were not included in the results, because they may have been missed in 1981. Inclusion of these trees magnified the observed trends, so the results presented are probably conservative. Based on L(t), clumping intensity decreased from 1981-1985, and the scale of maximal clumping became less distinct (Fig. 8). This trend was most pronounced in small trees (2.5-5.5 cm dbh), whereas there was no change for large trees ($\geq$5.5 cm dbh) (Fig. 8). The mean nearest neighbor distance increased from 1.35 m in 1981 to 1.40 m in 1985 for trees $\geq$2.5 cm dbh in the reference plot, and Donnelly's index indicated that trees were less clumped in 1985 (Table 4). However, when small and large trees were considered separately, Donnelly's index indicated a slight increase in clumping (Table 4).

Post-fire changes

There was 57.4% and 41.5% crown mortality from the fires in initial-A and initial-B, respectively, and in both fields the scale of maximal clumping decreased by more than 10 m for trees $\geq$2.5 cm dbh and also the 2.5-5.5-cm dbh class (Figs. 6 and 7). In post-fire initial-A, clumping intensity increased for trees $\geq$2.5 cm dbh and the 2.5-5.5-cm dbh

class, but intensity decreased slightly in post-fire initial-B. However, pre-fire clumping intensity was higher in initial-B than in initial-A, and the clumping patterns in both fields were more similar after their fires than before. Turkey oaks became randomly distributed beyond 27 m in initial-A; and although turkey oaks in post-fire initial-B remained clumped at large scale, the tendency was towards a more random pattern. Large oaks in post-fire initial-B remained maximally clumped at 12 m, but clumping intensity increased slightly from 0-20 m radius, and a more random pattern was observed from 20-30 m. A similar trend was observed for large oaks in post-fire initial-A, although sample sizes were small and both pre- and post-fire patterns were only marginally clumped based on the Monte Carlo tests (Fig. 6).

In both initial fields crown-killed trees $\geq$2.5 cm dbh were more intensely clumped at all scales than live trees before the fires (Fig. 9). Crown-killed trees in initial-A were maximally clumped at about 26-28 m, the same as for live trees, but another distinct peak also occurred for crown-killed trees at about 10 m radius. In initial-B maximum clumping occurred at 27 m, the same as for live trees. However, separate analysis on the north half of initial-B, where most of the large pines were concentrated, indicated that crown-killed turkey oaks were maximally clumped at 7 m (and also at 23.5 m) (n=132), compared to 11-

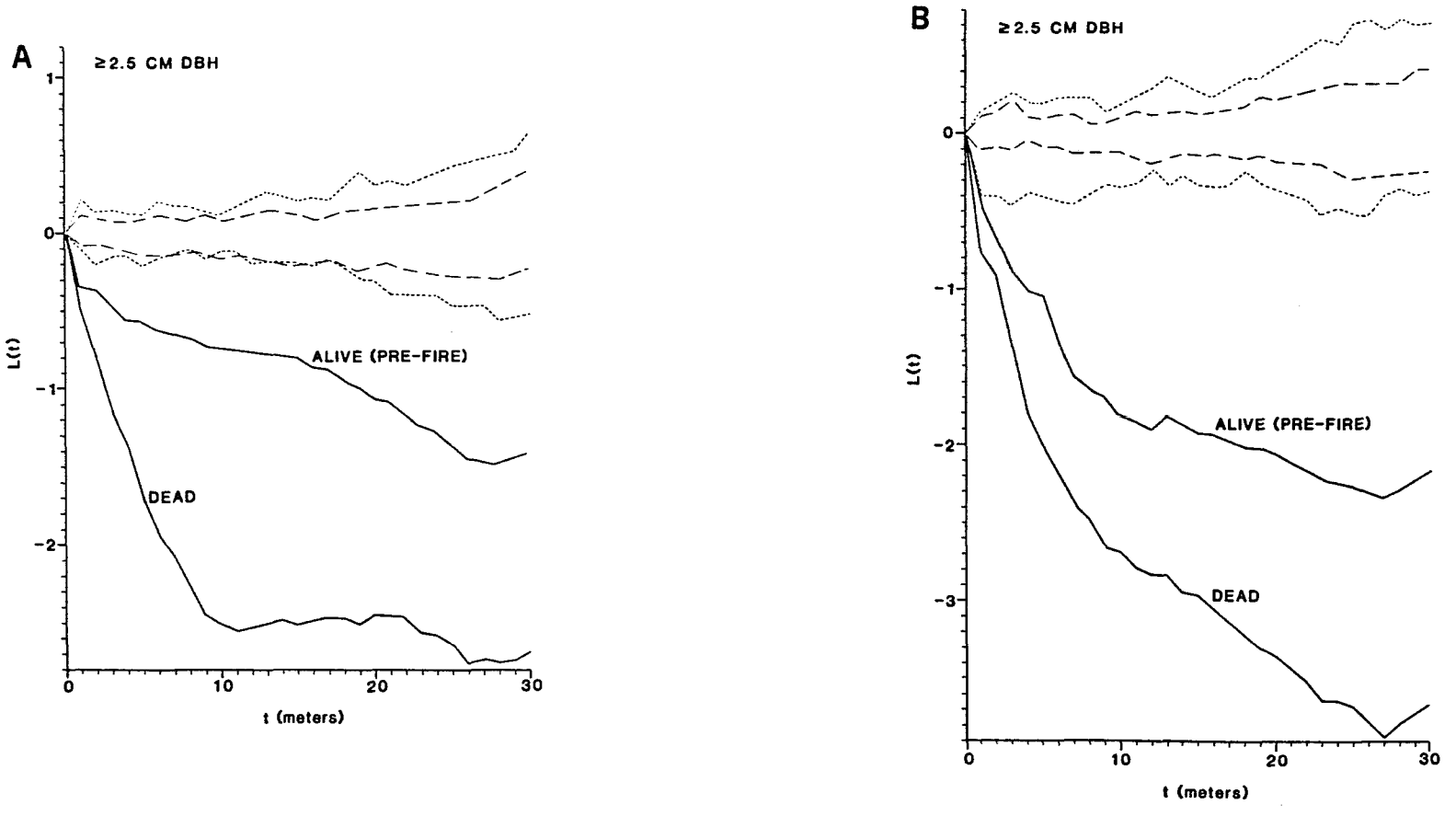



Figure 9. Ripley's L(t) plots for live (pre-fire) and crown-killed turkey oaks in initial-A (A) and initial-B (B) (see Fig. 6 for further explanation).

12 m for live trees (n=274).

The effects of repeated fires on turkey oak pattern in the 1, 2, and 5-year fields were similar to those in the initial fields: clumping intensity usually increased through the intermediate scale, and trees were randomly (or became more randomly) distributed at large scale. Previous fires had greatly reduced the number of small trees in these fields, so the documented changes reflected pattern mainly of large trees, which comprised from 55-92% of the population (Table 4).

In the 1-year field, the scale of maximal clumping decreased slightly (from 10 to 8 m) from burns 4-8 (Fig. 10). Clumping intensity increased substantially from burns 4-6 but increased only slightly from burns 7-8. Prior to burn 4, clumps in the 1-year field were already randomly distributed beyond 15 m. After burns 6-8, however, the upper range of clumping expanded to 19-21 m.

In the 2-year field, most of the turkey oaks in the plot interior were already killed prior to the third burn, and the remaining trees were intensely clumped in the vicinity of several large sand live oak groves (Fig. 11). The third fire increased clumping intensity from 0-26 m and created a more random pattern from 26-30 m. Turkey oaks were maximally clumped from 8-22 m prior to the third fire, but this peak was constricted to 10-15 m after the third fire. There was little change in the pattern of turkey oaks

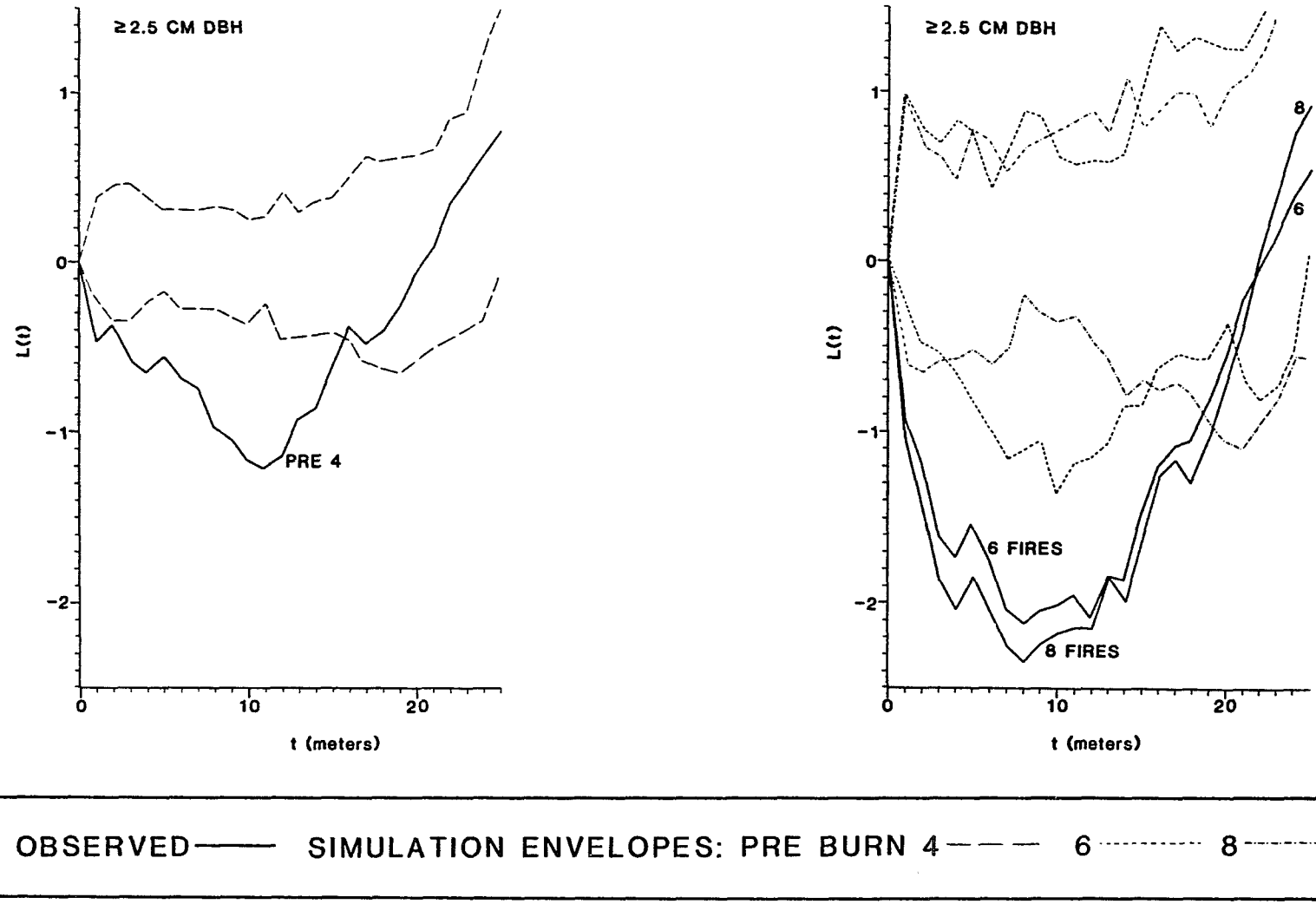



Figure 10. Ripley's L(t) plots for turkey oaks in the 1-year field prior to burn 4, after burn 6, and after burn 8 (see Fig. 6 for further explanation). Large trees (≥5.5 cm dbh) comprised 74%, 73%, and 75% of the population, respectively.

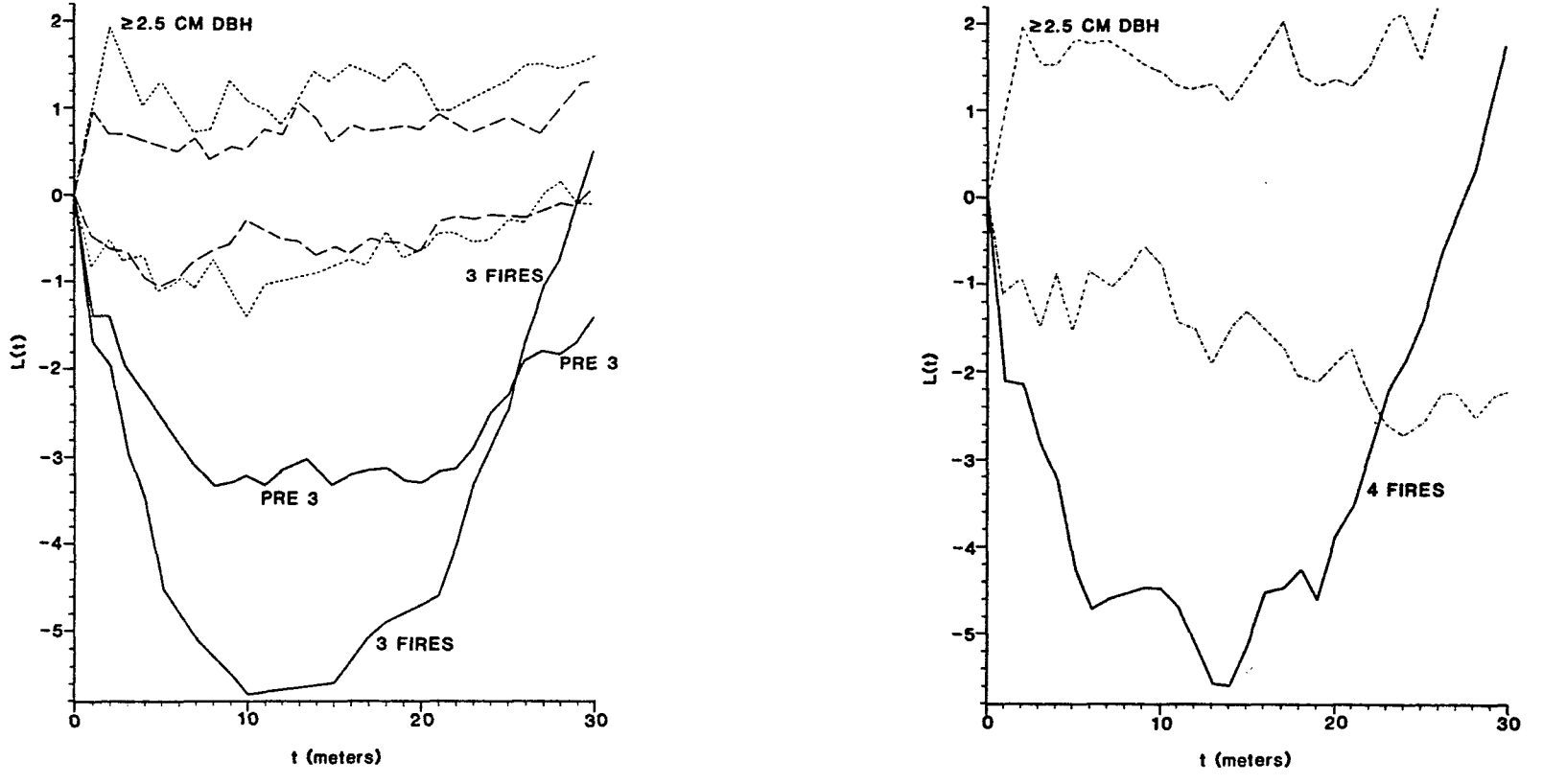



Figure 11. Ripley's L(t) plots for turkey oaks in the 2-year field prior to burn 3, after burn 3, and after burn 4 (see Fig. 6 for further explanation). Large trees comprised 68%, 79%, and 73% of the population, respectively.

remaining after burn 4, except the pattern was slightly more variable due to the lower sample size.

The pattern of turkey oaks in the 5-year field after 1 fire was very similar to both initial fields after 1 fire (Figs. 6, 7, and 12). A very distinct clump size of 7-m radius was recognizable, and clumps were uniformly distributed at large scale (Fig. 12). The second fire increased clumping intensity at ca. 7 m radius, while large-scale uniformity declined slightly relative to the upper bounds of the simulation envelope. The third fire killed most trees in the plot interior and left the pattern grossly altered. Clumping became more intense, mainly from isolated patches near the edge of the plot, but large-scale uniformity was completely gone.

The mean nearest neighbor distances increased after fires in the initial fields and after each fire in the 1, 2, and 5-year fields, but there was no consistent change in the overall pattern based on Donnelly's test statistic (Table 4). For example, trees $\geq$2.5 cm dbh in initial-A became more clumped, trees in initial-B became less clumped, and trees in the 2-year field went from less clumped (pre burn 3-burn 3) to more clumped (burn 3-burn 4).

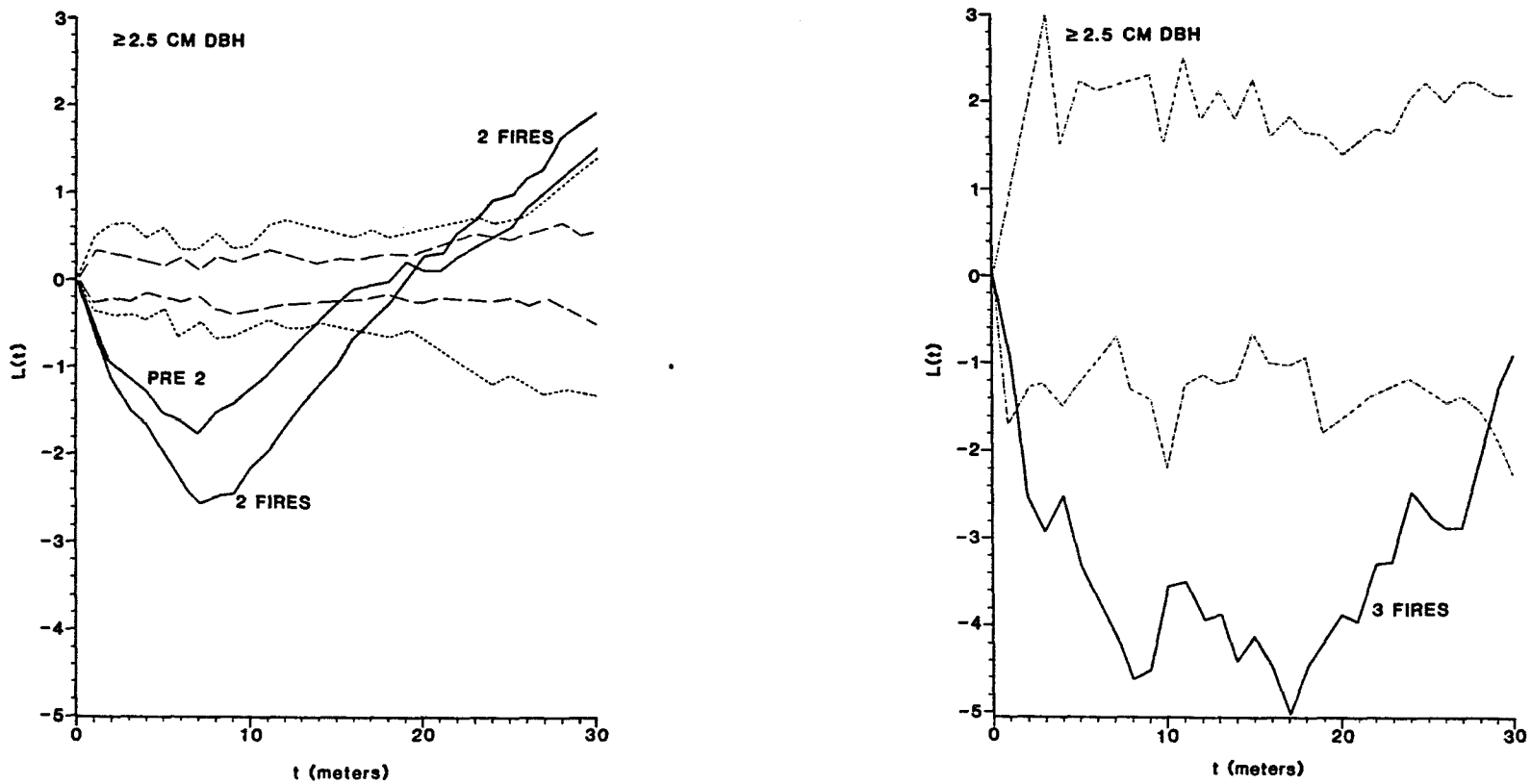



Figure 12. Ripley's L(t) plots for turkey oaks in the 5-year field prior to burn 2, after burn 2, and after burn 3 (see Fig. 6 for further explanation). Large trees comprised 55%, 63%, and 92% of the population, respectively.

# DISCUSSION

## Post-fire changes

Initial fires apparently had several immediate effects on the pattern of surviving turkey oaks:

(1) decrease in the scale of maximum clumping, i.e. smaller clump sizes

(2) increase in clumping intensity

(3) more random pattern at large scale.

There was some inconsistency for changes in overall pattern based on Donnelly's index, but nearest neighbor distances may give a deceptive view, especially when L(t) plots suggest that the effects of fire on pattern are scale-dependent. All of the above trends indicate that surviving turkey oaks were found in more discrete, isolated clumps after initial fires. Variability in this pattern was probably associated with the density and distribution of pines, variation in fire severity, and natural and man-made edge effects.

Given the conditions of no reproduction and random mortality, an initially clumped pattern should remain clumped over time (Kent and Dress 1980). If clumps are randomly distributed, however, thinning within clumps will eventually lead to a random pattern. Cooper (1961), who studied ponderosa pine, believed that surface fires selectively removed smaller, closely-spaced trees, leaving a

more random to uniform pattern. This process may have been partially responsible for some of the changes in pattern observed, but fire usually increased clumping intensity (despite high mortality), which suggests a different process of non-random mortality (cf. Gulmon and Mooney 1977).

Non-random mortality in sandhill fires is probably directly related to variation in fire intensity due to irregular fuel distribution, particularly near longleaf pines and sand live oak groves (Williamson and Black 1981). In the experimental fires, turkey oaks clearly suffered higher mortality near large longleaf pines. Crown-killed trees in initial-A were more clumped than live trees, especially at about 11 m (Fig. 9). Zones of nearly 100% turkey oak crown mortality extended from 5-15 m around a group of 9 pines in this field, which probably corresponds to the 11-m peak in L(t). Intense fire near the highly clumped pine grove essentially divided the turkey oak population in two. Most of the turkey oaks were 3-5 cm dbh and this size distribution, coupled with an exceptionally hot fire, contributed to high mortality near pines in initial-A. High fire mortality of turkey oaks near pines would leave surviving trees in patches between individual or groups of pines, which accounts for the post-fire shift towards smaller, more intense clumps that were randomly to uniformly distributed. High mortality around pines seemed to break up large, coalesced patches of turkey oaks into

separate, discrete clumps that were more evenly spaced. Interestingly, turkey oaks in the east half of initial-A, where there was only one pine, still suffered 47% crown mortality (94 of 199), yet pattern changed very little.

Crown-killed trees in initial-B were also much more clumped than live trees, although the shape of L(t) for live and dead trees for the entire field was basically the same (Fig. 9). This result may explain why turkey oaks in this field were not more intensely clumped after the fire: thinning within clumps was apparently extensive (Fig. 7). Bonnicksen (1975) pointed out that if small scale clumps have a higher density than areas that link clumps together, mortality will leave the smaller clumps more distinct. This process may account for the more random pattern of clumps at large scale in post fire initial-B (Fig. 7). However, crown-killed turkey oaks were maximally clumped at 7 m in the north half of initial-B, which roughly corresponded to clusters of mortality centered around one to several pines, so mortality patterns were still affected by pines even though this was not evident for the whole-field analysis. Pines may not have been as important as in initial-A, because there were more large turkey oaks in initial-B and the fire was milder (due to shading and less wiregrass).

Pattern in the 5-year field after the first and second fires was very similar to the post-fire patterns of both initial fields (Figs. 6, 7, and 12). The exceptionally

intense intermediate-scale clumping coupled with distinct large-scale uniformity probably was related to the contiguous distribution of pines and oaks. Initial fires left many surviving trees in patches between the pines, creating a complementary pattern between pines and oaks. Diggle (1983, p. 120) found similar complementary patterns among some hardwood species. After the second fire (5 yr later), the complex pattern in this field was already starting to erode. Small scale clumping became more intense, but large-scale uniformity started to decline as patches thinned out and became less discretely separated (Fig. 12). The dissolution of randomly or uniformly distributed clumps by thinning eventually leads to completely random patterns (Kent and Dress 1979, 1980). The third fire killed all but a few very large turkey oaks in the field interior, which magnified edge effects. Several turkey oak clumps survived in field corners and along firebreaks, where fires were probably milder, and the resulting pattern was dominated by these few, intense clumps. A similar process was apparent in the 1-year field (Fig. 10), but due to lower fuel loads and milder fires, many large oaks persisted in the field interior through 8 fires, and edge effects were only slightly noticeable. Some turkey oak clumps survived adjacent to sand live oak groves, which probably acted as natural firebreaks. Sandhill fires are relatively mild under sand live oak groves, which

inhibit wiregrass growth and produce a moist, incombustible litter (Williamson and Black 1981). In the 2-year field, substantial mortality in the field interior apparently occurred after just 2 fires. A few large, badly-scarred trees survived in isolated pockets between pines, but most of the turkey oaks persisted only near sand live oak groves. The scale of turkey oak clumping (a broad peak from 8-20 m) in the 2-year field after 3 fires (Fig. 11) closely mirrored the pattern of sand live oaks (see Chapter III). Turkey oaks seemed to have lower fire mortality in and around sand live oak groves, particularly in the 1 and 2-year fields, where some of the last remaining turkey oak clumps persisted near large sand live oak groves.

Since turkey oaks resprout vigorously, genet patterns will be more static than tree patterns. There were still >1500 genets/ha in the 1-year field after 8 fires, and the genet pattern closely resembled the distribution of trees (alone) after 1-2 fires: clumped from 1-13 m, random from 13-22 m, and slightly uniform from 22-30 m. This suggests that similar forces were affecting genet pattern, only more slowly. However, turkey oak resprouting ability is sometimes inversely related to the distance to the nearest pine (see Chapter I), so the effect of longleaf pine pyrogenicity on the pattern of turkey oak genets is potentially very different from its effect on trees.

Pattern and succession

In unburned fields there were approximately 2000 sprout clumps/ha, and many of these clumps represent suppressed turkey oak genets. When these clumps were included with trees, the pattern was still basically the same as for trees alone - clumped at all scales - only with less intensity. Stands in unburned initial-A were only slightly more clumped than the combined pool of trees and sprout clumps. This field had previously been burned three times over a 6-yr period, killing all but 30 trees, and regrowth was dominated by dense stands in the 2.5-5.5-cm dbh class. Thus, even-aged stands that develop after heavy post-fire release may approach the pattern represented by the complete pool of genets. After post-fire release, some patchiness probably develops in turkey oak stands due to edaphic factors or competition, but most patchiness probably results directly from variations in crown-mortality and sprout release from previous fires. Cooper (1961) recognized that pattern in ponderosa pine (Pinus ponderosa) was essentially a mosaic reflecting many past disturbances. Since fires near pines kill a high percentage of turkey oaks (Williamson and Black 1981), stands near pines will be younger and more even-aged than stands isolated from pines, where many large trees persist through fires. Thus, pines may affect pattern by influencing the structure of turkey oak stands.

The effects of fire on turkey oak distribution appear

to be in opposition to the forces of succession. The 4-yr changes in the reference field suggest that as stands mature and thin, clumping intensity declines, clumps become less distinct, and pattern becomes more random overall (Table 4, Fig. 8). Although the mean nearest neighbor distance for trees $\geq$2.5 increased over the 4-yr period, the mean nearest neighbor distances within small and large tree-classes actually decreased slightly. Apparently, changes in L(t) reflected mainly thinning among clumps, beyond the scale of nearest neighbor distances. After a fire, regrowth of crown-killed trees from basal sprouts would eventually fill in the voids left by fire, particularly near pines, and gradually clumps would coalesce into larger aggregations. Then, thinning of small, highly clumped turkey oaks (see Fig. 8) would leave remaining trees more evenly spaced. A decrease in clumping with succession has been reported for a variety of woody and herbaceous plants (Whitford 1949; Cooper 1961; Greig-Smith 1961, 1964; Laessle 1965; Bonnicksen 1975; Christensen 1977; Whipple 1980; Good and Whipple 1982).

Bonnicksen (1975) reported no differences in the pattern of sugar pine and white fir between burned and unburned plots, although he believed that pervasive regeneration from past fires was responsible for hierarchial clumping in some conifers. Cooper (1961) described fire as a "force that opposes the natural tendency of vegetation to

take on a random distribution." He found that fire was responsible for establishing even-aged stands of ponderosa pine in clumps associated with favorable regeneration on patches of bare mineral soil. Other disturbances may also create mosaic patterns. For example, Williamson (1975) found that the clump sizes of some early seral species corresponded well to the median size of treefall gaps in old growth beech-maple forest. In the New Jersey Pine Barrens, Gill (1975) believed that the "stochastic" forces of fire maintained random spacing among blackjack oaks (Q. marilandica), a species which is very similar ecologically to turkey oak. Gill believed that fire was a more potent force in determining pattern in blackjack oaks than biotic interactions or underlying substrate patterns. In contrast, the dynamic and opposing forces of longleaf pine pyrogenicity and sand live oak apyrogenicity in sandhill fires appear to be the main factors creating patchiness in turkey oak distribution. The most complex patterns of evenly-spaced, highly aggregated clumps seemed to develop after just 1 or 2 fires, with only simple, isolated clumps persisting after repeated fires. Likewise, turkey oak pattern eventually tended towards a simpler, more random pattern in the continued absence of fire. In this process, initial fires seem to prevent the competitive interactions that would eventually lead to simpler, more homogeneous stands. Diversity in many communities is related to the

intensity and frequency of disturbances (or predation), which set back the process of competitive elimination (Paine 1966, Connell 1978). In some tropical rain forests and coral reefs, diversity is highest at intermediate levels of disturbance (Connell 1978). Similarly, occasional fires may act as an "intermediate disturbance," maximizing spatial heterogeneity of sandhill vegetation.

Platt et al. (1988) also attributed the spatial segregation of adult longleaf pines and clumps of pine seedlings to the pyrogenicity of large pines. Although pine seedlings and turkey oaks are affected similarly by the intense fires near large pines, turkey oaks are still adversely affected by fire in areas where most pine seedling recruitment occurs. Shade trees sometimes improve the survival of longleaf pine seedlings (Gaines 1950, Allen 1954), so a slight overlap in the distribution of pine seedlings and turkey oaks may favor longleaf pine regeneration if interspecific competition is minimized.

# III. PATTERNS OF SAND LIVE OAK FIRE MORTALITY

# INTRODUCTION

Sand live oak is a clonal, grove forming tree found in well-drained sands along the Southeast Coastal Plain. Although not dominant in any community, sand live oaks inhabit communities with vastly different fire regimes, from a fire every few years in sandhill and flatwoods, every 20-50 yr in scrub, to very rare occurrence of fires in xeric hammocks (Pessin 1933, Miller 1950, Laessle 1958, Snedaker 1963, Richardson 1977, Abrahamson 1984, Givens et al. 1984, Myers 1985, Platt and Schwartz (in press)).

In xeric sandhills, sand live oak is subdominant to longleaf pine and turkey oak, both of which are well adapted to survive frequent surface fires. Longleaf pine has fire-resistant "grass" stage seedlings, and adults are well protected by fire-resistant bark and branchless lower trunks (Mattoon 1922, Platt et al. 1988). The well-aerated, highly combustible needle litter of longleaf pine is considered pyrogenic, or fire facilitating (sensu Mutch 1970), generating very intense fires near pines (Williamson and Black 1981). Large turkey oaks are fairly resistant to mild surface fires, and although small trees are vulnerable to fire damage, crown death is often followed by vigorous basal resprouting (Heyward 1939, McGinty and Christy 1977). Although sand live oak is a common component of fire-prone communities, its response to fire has not been closely

studied. In Florida's palmetto flatwoods, Abrahamson (1984) reported that the number of sand live oak stems doubled immediately after a fire, mainly from sprouting of small trees. Myers (1985) noted that sand live oaks invaded sandhills in the absence of fire. In some parts of Florida, sand live oak is primarily a component of the scrub community, and occasionally is codominant with sand pine (Miller 1950, Laessle 1958, Myers 1985).

Williamson and Black (1981) found that during sandhill surface fires, temperatures within sand live oak groves were typically 50-200 °C lower than under the canopies of turkey oaks and longleaf pines. Sand live oak groves inhibit wiregrass growth, a key fuel component in sandhills, and the oak leaf litter within the groves is relatively moist and incombustible. Surface fires frequently skirt the groves or skim through them, only charring the oak litter. These fire-retarding characteristics may help sand live oaks survive frequent sandhill fires, although this hypothesis has not been tested.

A major objective of this study was to gain a better understanding of the life history of sand live oak in relation to fire. Trends in sand live oak crown mortality and recovery were examined from density, size and age-class structure, and spatial pattern data collected from a field burned once, fields burned at 1- and 2-yr intervals, an unburned reference plot, and several groves outside the

study plots. I also tested several hypotheses concerning the fire-retarding characteristics of sand live oak groves. Specifically, I hypothesized (1) that larger groves would be more buffered from fire and experience lower mortality than small groves, (2) that trees at the grove periphery would be more vulnerable than trees in the interior, and (3) that grove fire-retarding effects may counteract the pyrogenicity of longleaf pines and result in lower mortality for sand live oaks than other sandhill hardwoods.

## METHODS

Experimental fire plots were established in the University of South Florida Ecological Study Area near Tampa. For this study we selected a 0.7-ha field burned once after having been unburned for at least 21 yr (designated "initial field"), a 0.5-ha field burned annually for 8 yr ("1-year field"), a 0.7-ha field burned every two years for 8 yr ("2-year field"), and a 0.8-ha reference field which was unburned for at least 21-25 yr. The 1-year and 2-year fields were censused completely, whereas 0.43-ha and 0.24-ha plots were censused in the initial and reference fields, respectively.

Complete tallies of all sand live oaks $\geq$2.5 cm dbh were made before and after the only fire in the initial field; after burns 4, 6, and 8 in the 1-year field; after burns 2,

3, and 4 in the 2-year field; and in 1981 and 1985, 21 and 25 yr unburned, respectively, in the reference field. The initial field was sampled 9 mo after the fire and also 4 yr post-fire to account for delayed mortality, while other fields were usually sampled from 7-9 mo post-fire.

Additional data from the 1-year field were obtained from a 107.5 by 3.5-m belt transect, which was sampled for trees $\geq$4 cm dbh before the first burn and after fires 1-4, 6, and 8. Densities could not be derived from this data because the transect deliberately bisected the two largest oak groves in the field, but the fate of individual trees could be monitored.

Regression analysis was used to examine the fit of dbh-class frequency distributions to the negative exponential (semi-log) and power function (log-log) models (Hett and Loucks 1976, Harper 1977). To examine the structure of young groves regenerating from past disturbances, age-class frequency data were collected from three groves consisting only of sprouts (maximum height 1.5-3 m). Age was determined from ring counts of sections cut from ground level to 10 cm. One grove was located in an unused section of the study area and was known to have been burned 1 yr and possibly 9 yr prior to its sampling. To determine age structure prior to the most recent fire, both live and dead stems were sampled from about one-third of the grove, and 1 yr was subtracted from the age of live stems. Post-fire

structure included stems which survived the fire, all resprouts from dead stems, and any new suckers. The other two groves were located within a few km of the study area and showed no evidence of recent fires. Both of these groves were censused completely.

For analysis of spatial pattern, trees $\geq$2.5 cm dbh were mapped before and after the only fire in the initial field; after fires 3, 4, 6, and 8 in a 0.32-ha plot in the 1-year field; and after fires 3 and 4 in the 2-year field. Vegetation prior to the third fires in the 1-year and 2-year fields was partially reconstructed from the older remains of crown-killed trees. The remains may have been slightly biased towards larger stems, which are more resistant to decay and less likely to be completely consumed by fire. Rectangular plots were required for analysis, so areas were selected within each field to maximize sample sizes and plot area. The reference field did not have enough sand live oaks for meaningful pattern analysis.

The spatial pattern of mapped trees was analyzed using Ripley's L function (Ripley 1977), as implemented in the program of Moser (1987). The L function is a second-moment spatial test which utilizes the distances from each point to all other points. Such tests are very sensitive to multiple scales of pattern and will reveal pattern within and among groves. Monte Carlo tests based on simulated random patterns were used to assess the departure of the estimated

L from the hypothesis of complete spatial randomness (see Diggle 1983). Bar charts were used to summarize the results of the observed L function and Monte Carlo simulations. Departure of the L function from the 95% confidence envelope for a random distribution was symbolically represented on the chart as either clumped or regular ($P \leq 0.05$). To assess changes in the intensity of clumping, peak negative L values and also changes in L relative to the lower 95% bounds of the simulation envelope were recorded. By adjusting L relative to the confidence limits for a random distribution, it was hoped that sample size effects could be reduced.

Logistic multiple regression (Walker and Duncan 1967) was used to model sand live oak crown survival. The SAS LOGIST procedure (Harrell 1983) fits the logistic multiple regression model to a single binary (0-1) dependent variable; for example, "0" for "crown-dead" and "1" for "crown alive." The assumption of the model is:

the probability that the ith observation is 1 is:

$$P(Y_i=1|X_{i1}, X_{i2}, \ldots, X_{ip}) = 1/[1 + e^{(-\alpha - \sum_{j=1}^{p} \beta_j X_{ij})}],$$

where $\alpha$ is the intercept, and the $\beta_j$ are the parameters associated with the p predictors. The following predictor variables were evaluated:

(1) sand live oak dbh

(2) distance from the perimeter of the grove

(3) distance from the nearest large (≥10 cm dbh) longleaf pine.

Stepwise and backward elimination techniques were used to select statistically significant predictor variables based on likelihood ratio criterion. Model predictive ability was assessed based on Somers' $D_{yx}$, concordance, percent of observations correctly classified, and R statistics (see Harrell 1983).

The hypothesized fire-buffering effect of position within a grove was tested in three groves consisting of 7, 20, and 25 trees in the 1-year field after burns 6 and 8. The distance from the grove's perimeter was measured two ways: (1) the distance from a tree to the outermost extent of sprouts defining the grove (not counting very isolated, outlying sprouts), and (2) the distance to the outline of a convex polygon formed by the outermost trees. The hypothesized fire-buffering effect of grove size was tested by linear regression of percent mortality within a grove versus number of trees in the grove for the initial, 1-year, and 2-year fields. Percent mortality was averaged for single trees or other small "groves" with more than one observation.

# RESULTS

## Density and factors causing mortality

The fire in the initial field had caused 19% crown mortality (15 of 78 stems $\geq$2.5 cm dbh) 4 yr after the fire, although there was only a 12% net loss due to the recruitment of 6 trees into the size class $\geq$2.5 cm dbh. The probability of crown survival was positively related to sand live oak dbh and distance to the nearest large (>10 cm dbh) longleaf pine in the logistic regression model ($P \leq 0.01$; Tables 5 and 6). The largest tree killed was only 5.8 cm dbh, and only 2 crown-killed trees were $\geq$4 cm dbh (Fig. 13). The average distance of crown-killed oaks from pines was 3.8 m $\pm$ 2.3 (n=15) compared to 8.2 m $\pm$ 4.3 (n=63) for oaks surviving the fire. Sixty-seven percent (10/15) of crown-killed oaks were within 4.5 m of a large pine, which is about the maximum crown radius of large longleaf pines on the study area. The regression model demonstrates the abrupt change in probability of crown survival from near zero to 1.0 as distance to nearest pine increases, and as dbh of the sand live oak increases (Fig. 14). In contrast, the non-clonal turkey oak exhibits less abrupt changes (Fig. 14).

The relationship between percent mortality within a grove and number of trees in the grove was not significant ($P>0.05$) for the initial field, although the sample size was

Table 5. Statistical evaluation of logistic regression models of sand live oak crown survival in experimental fire plots. Significance indicated by "*" ($P \leq 0.05$) and "**" ($P \leq 0.01$).

| Field | n | -2 log likelihood chi-square | Concordance | Somers' $D_{yx}$ | % correctly classified | R |
|---|---|---|---|---|---|---|
| Initial | 78 | 35.17 ** (2 df) | 0.81 | 0.62 | 91.0 | 0.67 |
| 1-year | 76 | 21.82 ** (1 df) | 0.77 | 0.54 | 77.6 | 0.40 |
| 2-year | 63 | 20.40 ** (1 df) | 0.89 | 0.79 | 85.7 | 0.45 |

Table 6. Statistical evaluation of logistic regression parameter estimates of sand live oak crown survival in experimental fire plots. Significance indicated by "*" ($P \leq 0.05$) and "**" ($P \leq 0.01$). Variable "DIST" is the distance to the nearest longleaf pine (m), and "DBH" is dbh (cm) of sand live oak.

| Field | Variable | Beta | Std. error | Chi-square (1 df) | R |
|---|---|---|---|---|---|
| Initial | intercept | -5.801 | 1.798 | 10.41 ** | --- |
| | DIST | 0.573 | 0.170 | 11.43 ** | 0.35 |
| | DBH | 0.925 | 0.343 | 7.26 ** | 0.26 |
| 1-year | intercept | -2.494 | 0.669 | 13.91 ** | --- |
| | DBH | 0.208 | 0.054 | 15.10 ** | 0.35 |
| 2-year | intercept | -3.104 | 1.423 | 4.76 * | --- |
| | DBH | 0.425 | 0.149 | 8.11 ** | 0.33 |

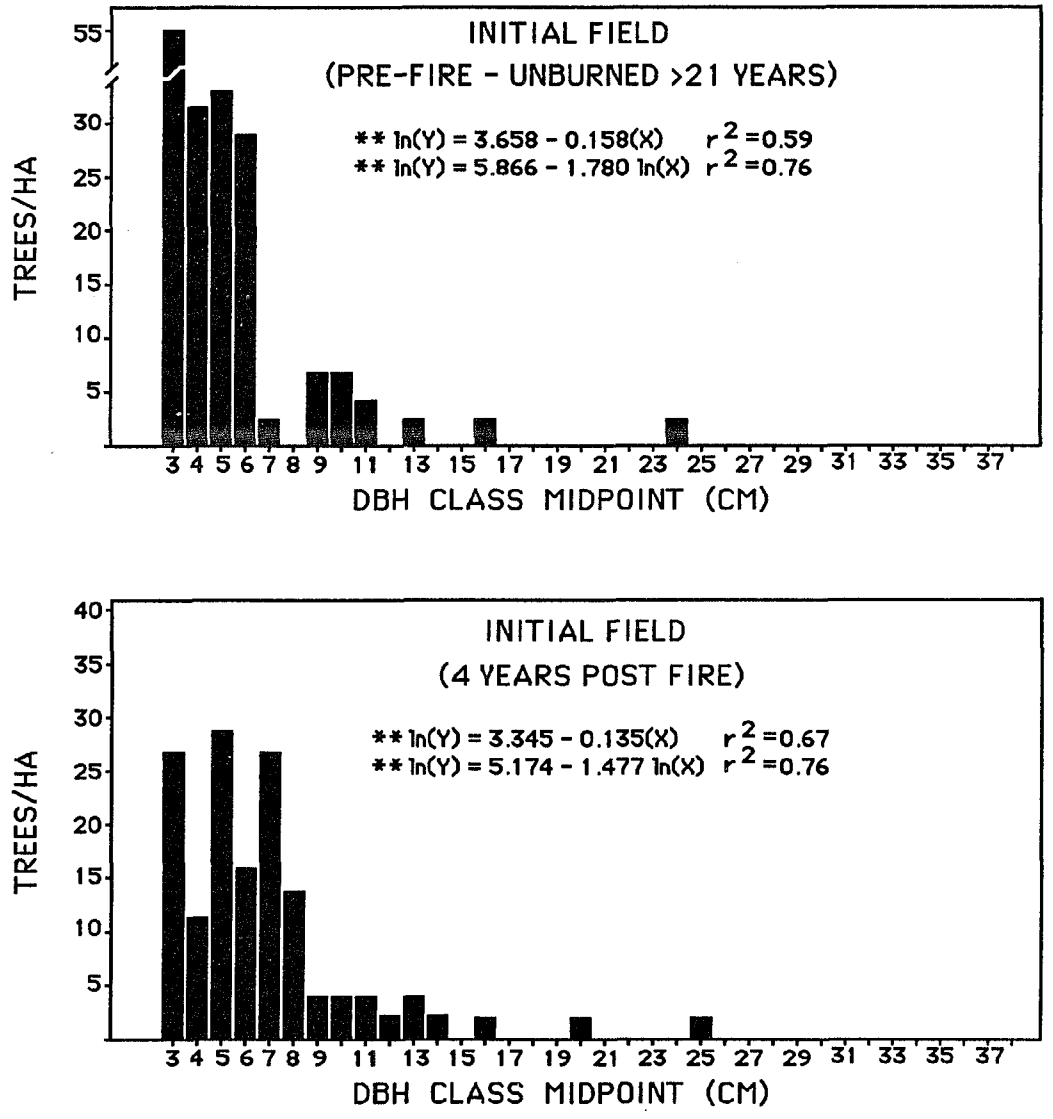



Figure 13. Size-class distributions of sand live oaks in pre- and post-fire initial field. Negative exponential and power function models are given for each distribution ("**" = $P \leq 0.01$).

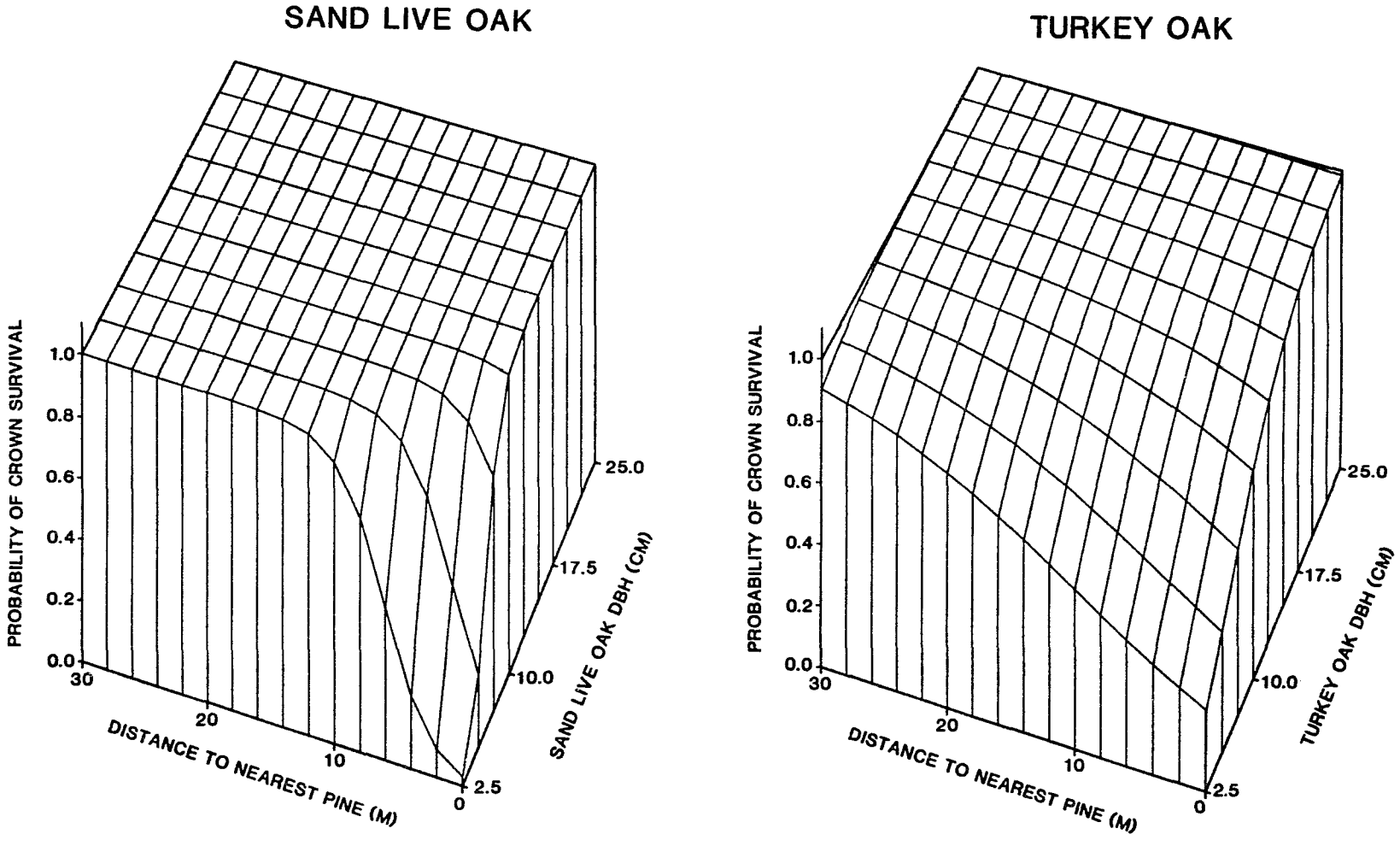



Figure 14. Logistic regression models for crown survival of sand live oaks and turkey oaks in the initial field. Maximum oak-to-nearest-pine distances are 21 and 19 m for sand live oaks and turkey oaks, respectively. Turkey oak results based on 39% crown mortality (185 of 473) from the same fire ($P \leq 0.01$ for logistic model).

small and included only one grove with more than 20 trees. The proximity of groves to pines probably explained some of the variation. For example, a grove of 7 trees, all more than 7 m from a pine, suffered no mortality; while a grove of 8 trees (about the same size as trees in the other grove), all less than 5 m from a pine, lost 3 trees. The largest grove had 24 trees and suffered no mortality, although the nearest pine was more than 8 m from the grove. In addition, grove size in the initial field was slightly correlated with dbh ($r=0.47$). Therefore most variation in mortality could be explained either by dbh or by the proximity to pines, and detecting a grove size effect was not possible.

Along the transect in the 1-year field, there was 67% mortality (16 of 24 trees $\geq$4 cm dbh) through the first 6 fires, but no trees were lost in fires 7 and 8. All the smaller trees (4-10.5 cm dbh) on the transect were dead after 6 fires, whereas none of the larger trees ($\geq$10.5 cm dbh) had died through 8 fires. For the entire 1-year field there was 51% mortality (46 of 90 trees $\geq$2.5 cm dbh) in fires 4-6, while only a single tree was lost in fires 7 and 8. Most trees in the 2.5-4.5-cm dbh range were already gone after 3 fires, and fires 4-6 alone caused 77% mortality (27 of 35) in the 2.5-10.5-cm dbh class, leaving only 8 trees in this size class (Fig. 15). Large trees (>10.5 cm dbh) had 35% mortality (19 of 55) in fires 4-6, but only one large

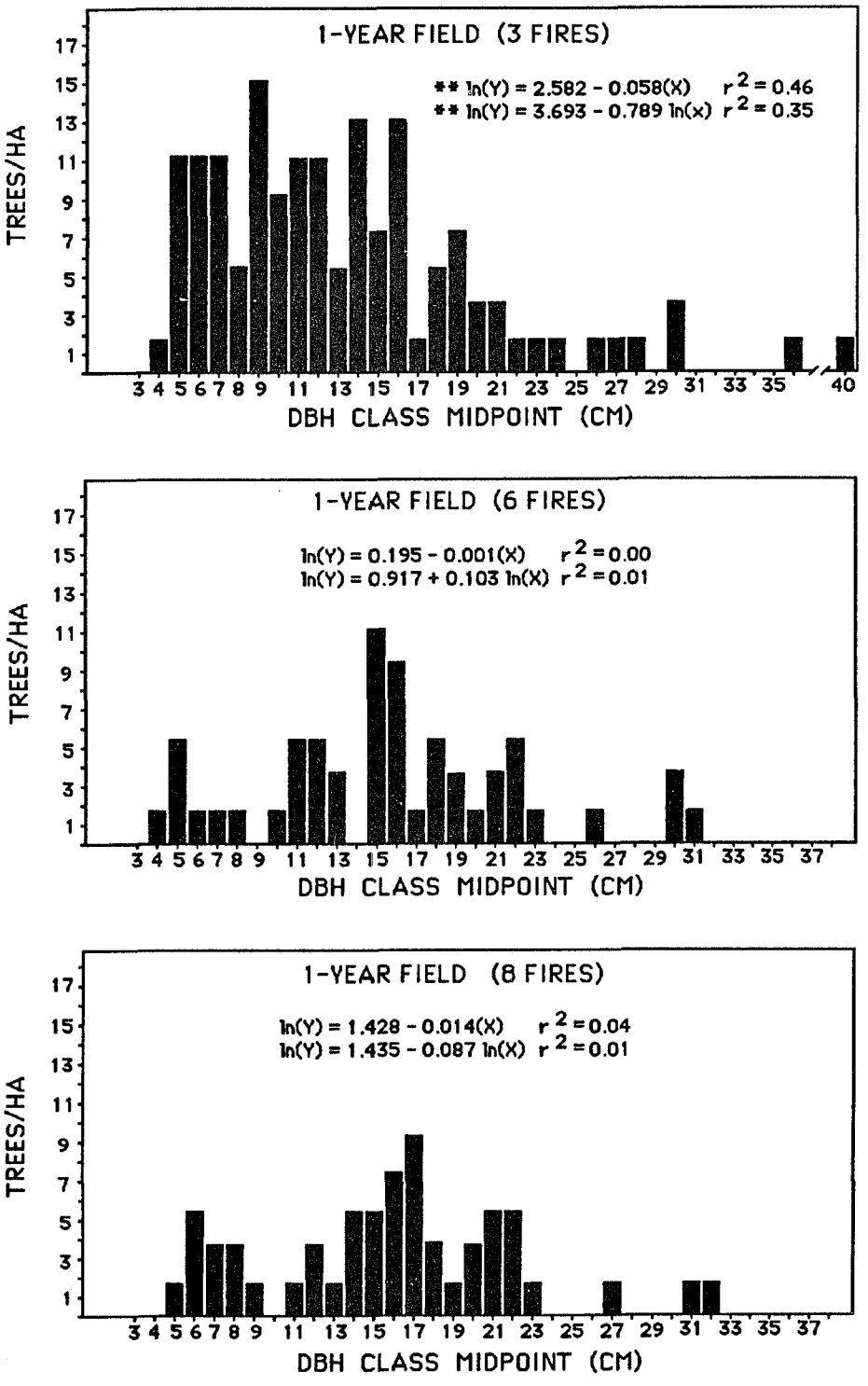



Figure 15. Size-class distributions of sand live oaks in the 1-year field. Negative exponential and power function models are given for each distribution ("**" = $P \leq 0.01$).

tree was crown-killed in the last two fires. In the mapped section of the field, fire-killed stems from burn 3 (and perhaps earlier) had an average dbh of 6.7 cm $\pm$ 1.8 (n=8), but this sample was probably biased towards larger, more persistent stems. In fires 4-8 the average dbh of crown-killed trees increased to 10.0 cm $\pm$ 4.3 (n=25), including 2 trees larger than 18 cm dbh. No seedling or sprout recruitment (into the small-tree class) was observed since annual burning began.

The only significant variable in the logistic regression model for the 1-year field was sand live oak dbh ($P \leq 0.01$; Table 6). Longleaf pines and sand live oaks were well separated in this field prior to prescribed burning, so there was little opportunity for interaction. Although many isolated and small groups of trees experienced high mortality, again there was no consistent relationship between crown survival and grove size. For example, all but 2 trees in a grove of 20 were killed in fires 3-8, while 20 m away in a grove of 25 trees only 7 trees were killed during the same period. In this particular comparison, dbh explained nearly all of the mortality (small trees died and large ones did not), whereas grove size did not seem to matter. There was also no consistent relationship between crown survival and distance from the grove perimeter. Mortality appeared to be concentrated at the periphery of some groves but not in others. Most of the variation in

crown survival within a grove, however, could be explained by dbh alone.

In the 2-year field, mortality patterns were similar to those in the 1-year field. After two fires most of the trees in the 2.5-4.5-cm dbh range were already gone (Fig. 16). The third fire caused 46% mortality (47 of 103), and almost all of the trees killed were in the 2.5-10.5-cm dbh class, which declined by 79% (45 of 57). There was only 5% mortality (3 of 56) in the fourth fire, all less than 10.5 cm dbh, leaving just 9 small trees in the entire field. No seedling or sprout recruitment (into the small-tree class) was observed in this field.

The only significant variable in the logistic regression model for the 2-year field was sand live oak dbh ($P \leq 0.01$; Table 6). Most of the oak groves were located far from pines, but a few oaks at the north end of the field may have been adversely affected by the locally intense fires around pines. Many isolated trees and small groves suffered mortality, but again there was no consistent relationship between crown survival and grove size. For example, in one grove at the eastern end of the field, only 2 of 16 trees survived 4 fires, while observed mortality was less than 40% for two large groves at the western end. Three sand live oak groves and one Q. virginiana grove apparently were completely burned up prior to mapping, leaving only sprouts. Since no identifiable stems remained in these groves, they

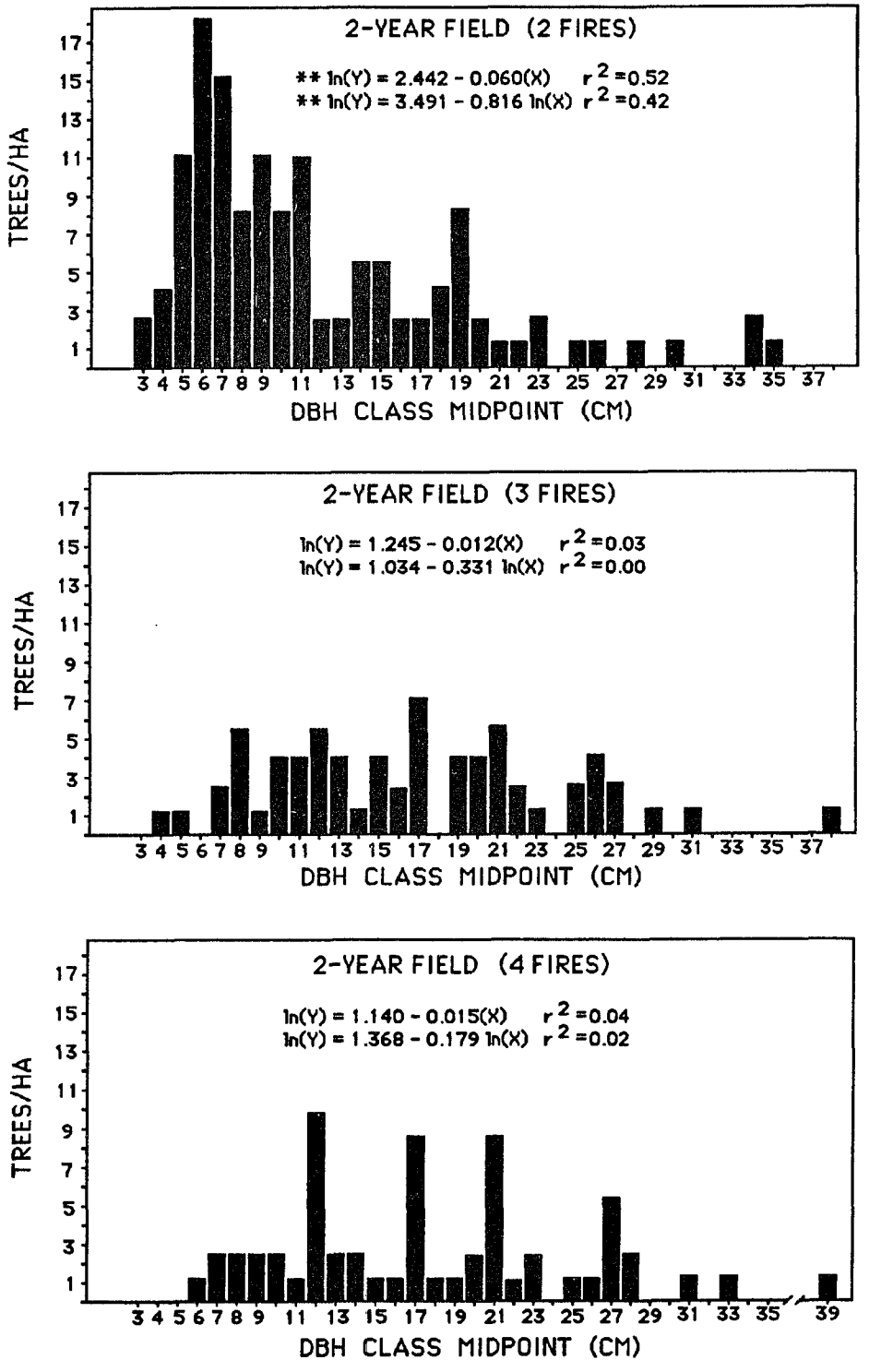



Figure 16. Size-class distributions of sand live oaks in the 2-year field. Negative exponential and power function models are given for each distribution ("**" = $P \leq 0.01$).

probably consisted of a few, small-diameter trees.

In the reference field, which was unburned for at least 21 yr, the population of trees ≥2.5 cm dbh increased by 31% (from 16 to 21) between 1981 and 1985. There was no mortality and 5 trees were recruited during this time.

Size-class structure

In the pre-fire initial field the size-class structure was described fairly well by the power function and by the negative exponential function (Fig. 13). The power function had a slightly better fit, but larger sample sizes and the inclusion of sprouts probably would have improved the negative exponential model. The structure of the initial field had changed very little 4 yr after the burn, mainly because mortality in smaller size-classes was partially offset by recruitment of young trees, and growth of some trees in the 3.5-6.5-cm dbh range evened the distribution slightly (Fig. 13). Again, the size distributions significantly fit both functions (Fig. 13).

Repeated fires in the 1-year and 2-year fields killed most of the small trees, and their size-class structures became disjointed, somewhat bell-shaped, and poorly described by both the negative exponential and power functions (Figs. 15, 16). However, it is noteworthy that the size distributions fit both functions even after several fires (3 in the 1-year field and 2 in the 2-year field), and

only after repeated burns were both functions insignificant. The structure of both fields after repeated fires appears to be multimodal, with peaks in the 11-13, 15-17, 20-22, and 26-28-m ranges. The first peak (intermediate dbh range) may simply be an artifact of the massive removal of smaller trees; however, peaks in larger size-classes were probably inherent to the population prior to the experimental fires. Peaks did not correspond to trees from a single grove. For example, the 26-28-cm dbh oaks in the 2-year field belonged to five different groves.

Age-class structure

The three young, regenerating groves (Fig. 17) have age structures suggesting recovery from past fires or other disturbance. Grove A, for example, was in the vicinity of an area known to have been burned in 1968, which also corresponds to the age of the oldest stems in the grove at the sampling time (1977). Prior to the most recent (1976) fire, the age-class distribution fit both the negative exponential and power functions reasonably well. The post-fire structure was adequately described by both functions (despite the additional inclusion of resprouts), but $r^2$ was slightly higher for the power function. The age-class structure of grove B, which had no indication of recent fire, also fit both functions (Fig. 17). Grove C had large cohorts of 1 and 9-year-old stems, and an age structure

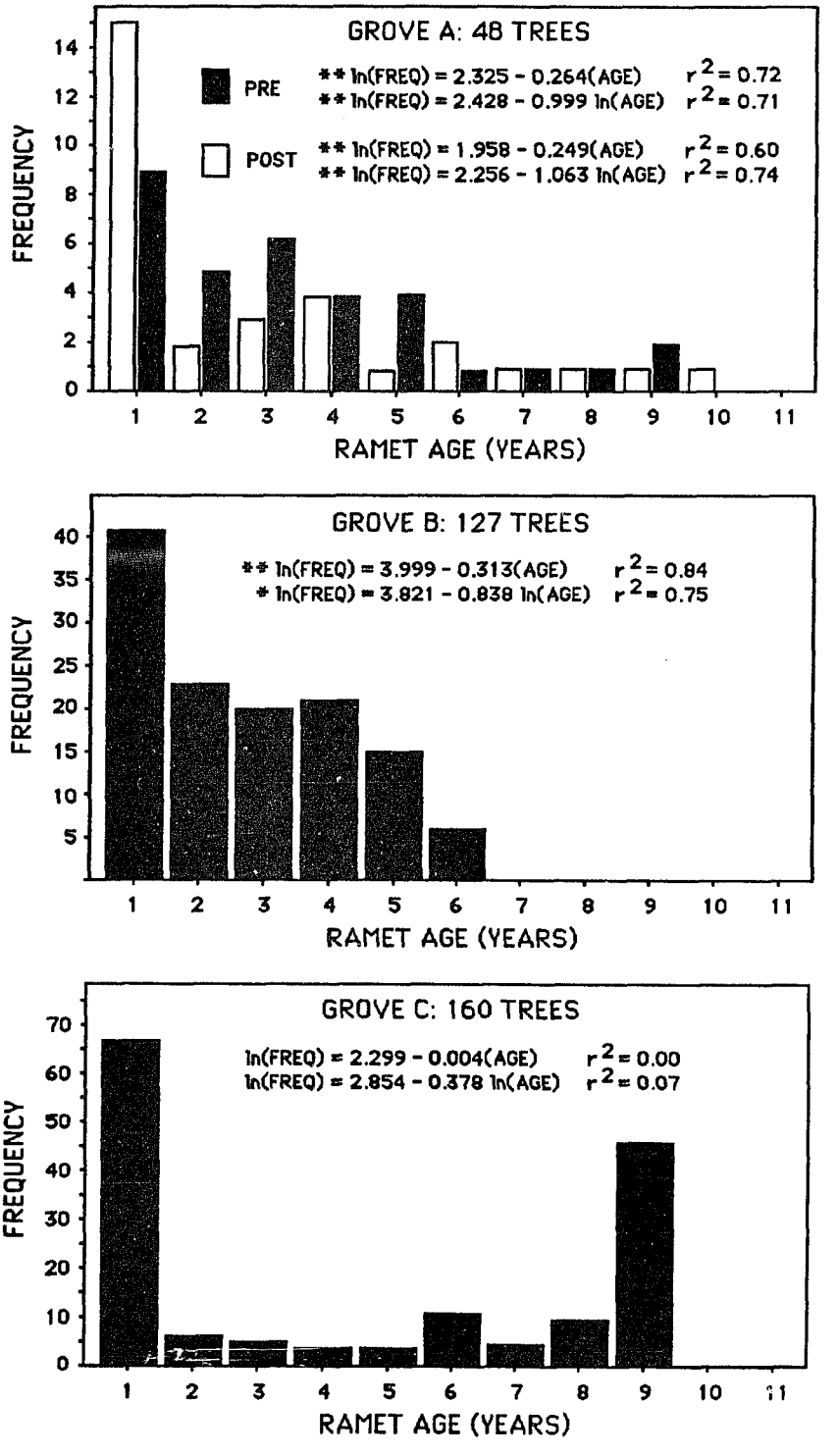



Figure 17. Age-class distributions of regenerating sand live oak groves. Grove A was burned 1 year prior to sampling, and pre- and post-fire distributions are given. Negative exponential and power function models are given for each grove ("*" = $P \leq 0.05$, "**" = $P \leq 0.01$).

which fit neither the negative exponential nor power function models (Fig. 17). Most of the 1-year-old sprouts and younger stems were located at the grove's periphery, where brushy hammock vegetation was crowding the grove.

Spatial pattern

Ripley's L indicated that trees were clumped at most scales in all three burned fields (Fig. 18). Maximal clumping in all three fields occurred at a scale of 6-8 m, which corresponds to the radius of many groves in the study area. A second maximum peak in clumping at larger scale (19-22 m) in the 2-year field reflected the clustering of several groves together in one area of the field (Fig. 18). Sand live oaks in the initial field (pre-burn) and 2-year field were hierarchically clumped from 0-30 m in scale; that is, trees were clumped into groves, and groves were clumped into progressively larger aggregations up to 30 m radius (Fig. 18).

The scale of maximal clumping changed very little after fires in all fields. However, the intensity of clumping (at 6-8 m) consistently increased after fires (Table 7). Successive fires in the 1-year and 2-year fields also resulted in more distinct peaks in maximal clumping (Fig. 18). For example, a broad peak from 4-9 m prior to the third fire in the 1-year field was reduced to a distinct

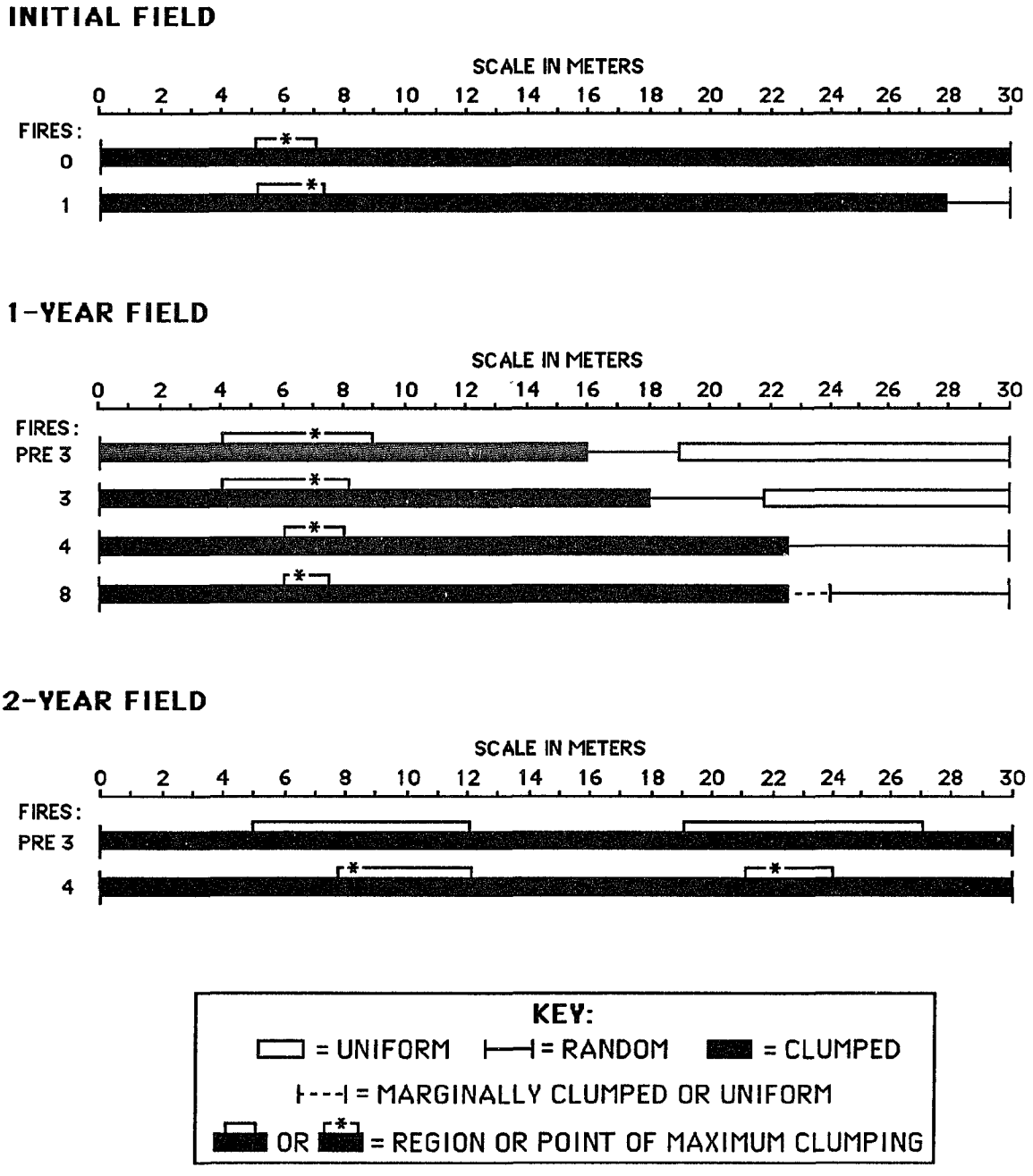



Figure 18. Spatial pattern of sand live oaks in experimental fire plots. Clumped and uniform patterns represent significant departure from randomness ($P \leq 0.05$), based on Monte Carlo tests.

Table 7. Changes in sand live oak clumping intensity with experimental burning in Florida sandhills. The more negative the value of Ripley's L, the greater the intensity of clumping. Deviation from randomness adjusts L relative to the lower 95% confidence limit for complete spatial randomness (see METHODS).

| Field | Number of fires | Minimum L | Scale (m) | Net change in deviation from randomness |
|---|---|---|---|---|
| Initial | 0 | -8.7 | 6 | --- |
| | 1 | -10.7 | 7 | -2.0 |
| 1-year | pre 3 | -4.1 | 7 | --- |
| | 3 | -4.3 | 7 | -1.1 |
| | 4 | -5.7 | 7 | -1.7 |
| | 8 | -7.5 | 7 | -1.4 |
| 2-year | pre 3 | -6.6 | 8 | --- |
| | 4 | -7.6 | 8 | -0.7 |

peak at 6-8 m after the eighth fire. Clumps became more randomly distributed at large scale (28-30 m radii) after the fire in the initial field (Fig. 18). Clumps were uniformly distributed beyond 19 m in the 1-year field prior to the third fire, but continued annual burning progressively eroded large scale uniformity and led to a more random distribution of clumps (Fig. 18).

## DISCUSSION

### Factors influencing sand live oak mortality

Stem diameter was consistently the most important factor determining sand live oak survival in sandhill fires. Sprouts and small trees (2.5-5.5 cm dbh) were vulnerable to initial and repeated fires, and successive fires have slowly removed progressively larger size classes. Since most of the smaller trees have died in the 1-year and 2-year fields, the population sizes have reached a plateau or are slowly declining. Because many of the large oaks are fire-scarred, they may succumb to subsequent fires more rapidly. It is well known that fire tolerance in hardwoods increases with stem diameter (McCarthy and Sims 1935; Heyward 1939; Harrington and Stephenson 1955; Ferguson 1957, 1961; Williamson and Black 1981) Fire resistance increases as trees become larger, the bark thickens, and sensitive crowns grow above the level of surface fires (McCarthy and Sims

1935). Bark thickening of larger stems is quite apparent in sand live oak: young stems up to 2-3 cm dbh are covered by a skin-like, photosynthetic bark which is vulnerable to fire, whereas larger stems have a rough, corky bark which may be several cm thick.

Fire mortality based solely on grove size and location of trees within a grove was highly variable, and in many cases the results were very unpredictable. In the same fire, groves of nearly identical size and structure might suffer little mortality or be completely devastated, depending on local variation in fire intensity and chance. Groves seem fairly resistant to fire intensities up to a certain threshold, beyond which foliage ignition occurs and kills or damages most trees in a grove. Once a few large stems are killed, their litter and the additional grass growth from light penetration may accelerate loss of other trees in successive fires. The observed variance in crown survival is probably indicative of the stochastic nature of grove responses to fire. Clearly, study of many more groves is needed.

The intensity of fire in proximity of pines adversely affected the survival of sand live oaks in the initial field, where pines and oaks were contiguous. No significant effect of proximity to pines was found in the 1-year and 2-year fields because there were very few sand live oaks within 10 m of large pines. In these latter fields, our

records cover mortality only in the more recent burns, not the initial burns, so the absence of sand live oaks near large pines is probably more than coincidental--i.e., sand live oaks in the vicinity of pines may have been eliminated in earlier burns.

In the initial field, sand live oak's sensitivity to pines was restricted mainly to smaller trees located directly beneath the pine's crown (ca. 4 m radius) or very near its perimeter. Turkey oaks, which do not form groves, also exhibit sensitivity to the hot fires near pines, but in contrast to sand live oaks, the effects of distance and dbh on the probability of crown survival change very gradually over 20 m of distance and 20 cm of dbh (Fig. 14). The different responses may reflect the buffering effect of groves in sand live oak versus the solitary individuals in turkey oak.

What factors contribute to produce the grove effect? First, wiregrass does not grow inside the groves, perhaps a result of competition for light or nutrients or maybe of interference. Second, dense evergreen foliage combined with low hanging branches of peripheral stems prevent light penetration and create relatively moist conditions within the grove. Finally, sand live oak litter is compact, moist and relatively incombustible. The buffering effect of the groves may counteract the pyrogenic effect of pines and wiregrass and thereby allow sand live oaks to persist with

pines in the sandhill. However, the degree of buffering is likely to be quite variable. For example, sand live oaks located directly beneath pines accumulate dead pine needles in their crowns and are acutely vulnerable to surface fires that explode into their crowns. Furthermore, increasing the frequency of fires diminishes the grove's buffering capacity: fires prune low-hanging branches and peripheral sprouts, allowing some colonization by wiregrass. Thus, successive fires at short intervals may turn a compact, highly buffered grove of many stems of various sizes into a few surviving, large individuals. Fires at longer intervals might allow significant regrowth after each fire. By moderating fire temperatures, sand live oak groves may also enhance the survival of other fire-sensitive plants growing in or near the groves. Turkey oaks and bluejack oaks seem to have persisted longer through repeated fires in the 1-year and 2-year fields if they were located near sand live oak groves.

Pattern

Because at least some of the large groves within each field remained intact, there was little change in the scale of maximal clumping after fires (Fig. 18). Although the scale of maximal clumping did not change, there was a consistent increase in the intensity of clumping, reflecting greater departure from randomness (Table 7). High mortality

of isolated trees and grove outliers was probably responsible for the increased clumping, or it may reflect the persistence of a few large groves, which simply became more distinct patches when other groves were eliminated.

Sand live oaks were originally clumped at all scales in the initial field, but they became more randomly distributed at large scale after the fire, indicating that the remaining groves were more distinctly separated (Fig. 18). The removal of a few isolated trees, grove outliers, and high mortality in smaller groves probably contributed to this change in large scale pattern. Subsequent thinning within proximate groves would tend to erode the spatial discreteness of clumps (Kent and Dress 1980). This probably caused the loss in uniformity observed in the annually-burned field (Fig. 18). Thinning in groves, particularly one large grove, left remaining ramets less associated with discrete clumps. Because sand live oak groves are extremely patchy, the areas sampled were too small to give an accurate representation of large scale pattern. Nevertheless, the observed changes in large scale patterns suggest trends which may occur locally.

Demography

The negative exponential function generally provides a good model of population structure when there is constant mortality and a relatively stable number of individuals

(Meyer and Stephenson 1943; Deevey 1947; Hett and Loucks 1971, 1976; Harper 1977). Although the pre-fire initial field was adequately described by the negative exponential function, a better fit was obtained with the power function, which implies a variable mortality rate decreasing with size (Deevey 1947; Hett and Loucks 1971, 1976; Leak 1975). Schmelz and Lindsey (1965) attributed the lack of negative exponential form in the structure of Indiana forests to disturbance, and our results confirm that the disproportionate removal of smaller trees by fire eventually leads to a highly disjointed, somewhat bell-shaped, size distribution which is poorly described by both the negative exponential and power function models.

Abrahamson (1984) reported that the number of sand live oak stems doubled immediately after a fire in the Florida flatwoods. Sand live oaks are extremely resilient in their recovery from fire, but the age structures of the three recovering groves indicate that regeneration may be fairly complex. The structures of both groves A and B were adequately described by the negative exponential function. This implies that sprouts were produced and died at a relatively constant rate since the original disturbance. This is consistent with the structure of other clonal plants, such as Picea mariana, which reproduces mainly by layering (Legere and Payette 1981), and rhizomatous Viola blanda (Cook 1983). Stability in the structure of clones is

maintained by the simultaneous senescence of older ramets and the development of younger ones (Cook 1983). Surprisingly the recent fire in grove A resulted in only as many new sprouts as were lost in the fire. However, this was only a single fire, and the magnitude of resprouting probably depends on both genet and ramet size and age, as well as timing and severity of the fire (Blaisdell and Mueggler 1956, Kayll and Gimingham 1965, Lacey 1974, Kellman 1986). The large cohort of 9-year-old stems in grove C represents the recovery of a large group of resprouts from fire, or a flush of new sprouts coupled with resprouting from dead ramets. Some new sprouts have been produced near this grove's perimeter every year since the fire, but apparently few have survived competition from encroaching vegetation. Presumably only a few of the current 1-year-old stems would survive another year. A similar age structure from undisturbed wolfberry (Symphoricarpos occidentalis) clones in the northern Great Plains approximates negative exponential depletion; however, the oldest ramets in burned clones comprise a massive cohort of post-fire resprouts, and a few sprouts are added in subsequent years (Pelton 1953). These results suggest that the age structure developed during fire-sensitive regenerating phases may be manifested in the structure of mature sand live oak groves.

Holland (1969) found that young stands of mallee Eucalyptus were generally even-aged, representing post-fire

regeneration from lignotubers, but subsequent thinning of these stands led to a bell-shaped structure similar to that observed in mature sand live oak groves which have been repeatedly burned. Multimodal age structures have been attributed to waves of recruitment associated with past disturbance (Peterken and Tubbs 1965, Lorimer 1980). The multimodal structure of sand live oak size-class distributions may reflect periodic damage to all or parts of groves resulting in pulses of resprouts/sprouts. If these waves of regeneration passed through fire-sensitive stages, then they would be represented as distinct cohorts. It is probably not coincidental that several peaks in the 1-year and 2-year fields correspond, since the responsible fires would have occurred long before the fields were separated, and the current experimental fires have not greatly affected their growth yet.

Sandhill succession

Prior to settlement most sandhills probably burned once every 3-4 yr (Chapman 1932). If fires have high frequency and periodicity, then longleaf pine savanna is favored and hardwoods would be a minor component of the vegetation (Snedaker 1963). Myers and White (1987) believed that when sand live oak is common in sandhills, it indicates a lack of fire. Long fire-free intervals (10-20 yr) and a nearby seed source probably are required for the establishment of sand

live oak; however, these results indicate that once it becomes established, it is extremely fire resistant and will persist through repeated fires at short-intervals (see also Platt and Schwartz (in press)).

Sand live oak's ability to survive under the harsh sandhill fire regime is favored by its flexible growth responses: (1) continuous sprouting or suckering, (2) resprouting from dead ramets, and (3) fire-resistant adult trees. Groves exposed to surface fires may lose smaller diameter stems, but large stems are lost only infrequently. Small stems are regenerated and suckering occurs annually, so any fire-free period longer than 6-8 yr may allow sand live oak groves to expand substantially. Expansion may further buffer the grove against fire intensity, so eventually several fires at short-intervals may be needed to burn a grove back. When all trees are killed, clones can apparently sustain themselves for many years in a creeping, shrub-like form despite repeated fires.

If fires become infrequent, groves may expand, fuse, and given a very long fire-free period, hammock-like vegetation may develop. Fire prevention is an important factor in the development of hammocks, and once established, fuel conditions often prevent mild surface fires from spreading into the grove (Harper 1911, Veno 1976, Richardson 1977, Platt and Schwartz (in press)). However, Platt and Schwartz (in press) suggest that rare, high-intensity fires

during periods of drought may convert hammock vegetation to more open pinelands. Sand live oak is also the only sandhill tree that is a common component of Florida's scrub community, the plant association Webber (1935) described as "a fire-fighting machine." Scrub burns only once every 20-50 yr (Richardson 1977). Continuous sprouting of sand live oaks during long fire-free periods in scrub (and xeric hammock) would promote genet longevity by balancing the loss of senescent stems. The ability of hardwoods to resprout generally decreases with tree size (Heyward 1939, Williston 1949, Ferguson 1957, Woods and Cassady 1961), so a continuous stock of young, vigorous sand live oaks probably favors successful post-fire resprouting.

The capacity of Australian Casuarina and Eucalyptus to maintain fire-resistant adult trees combined with resprouting ability is thought to broaden the range of fire frequencies under which these trees can survive (Kellman 1986). This flexibility allows these genera to dominate sclerophyll woodlands with intermediate fire frequencies or higher frequencies that are somewhat variable (occasional long fire-free periods). Malanson and Westman (1985) found that shrubs capable of both continuous basal sprouting and post-fire resprouting were more abundant in coastal sage scrub than in chaparral. They believed that continuous sprouting allowed short-lived shrubs to persist during the long fire-free periods characteristic of coastal sage

communities, and thus the plants resist overtopping and replacement by other species.

Sand live oak appears to have a great flexibility for surviving under different fire regimes. Since the successional relationships between sandhill, scrub, and hammock are poorly understood (reviewed by Veno 1976, Givens et al. 1984, Myers 1985), the origin of the growth habits of sand live oak are only speculative. The flexible response to fire may have evolved in response to frequent but somewhat variable fires, or the gradual expansion of sand live oak into new communities with vastly different fire regimes. There has been ample opportunity for selection of a "generalist strategy" in sandhill, scrub, and hammock communities, which are sometimes separated by very narrow ecotones.

# SUMMARY AND CONCLUSIONS

The conclusions presented here are unique in studies of fire ecology in that the study plots were controlled under a regimen of prescribed burning for a period of 9 yr with an additional 6-15 prior years of known fire histories. Plots burned at 1, 2, and 5-yr intervals, as well as some plots burned only once, were represented and compared to a reference plot unburned for 21-25 yr. Sequential sampling of plots allowed a view of the historical changes in fields of different rotations in addition to the more classical, "snapshot" of the current differences; in this regard, the vectors of pathways of change were as revealing as the current plot differences attributable to the fire regimes.

Turkey oaks suffered high crown mortality from intense fires occurring near longleaf pines, which produce a highly flammable litter. Small turkey oaks were even adversely affected 10-20 m from the nearest pine, far beyond the perimeter of the pine's crown. Although crown survival was positively related to the proximity of the nearest pine, in one fire resprouting ability of crown-killed trees was inversely related to the proximity of pines. Pyrogenicity favors longleaf pine as long as frequent fires keep turkey oak stands burned back, but pyrogenicity may favor turkey oaks if fires become infrequent or irregular because resprouting is enhanced near pines.

Turkey oaks (trees and genets) were slightly clumped at most scales in unburned fields. After initial fires, turkey oaks were generally found in smaller, more intensely aggregated clumps that were more randomly distributed at large-scale than before the fire. The patchiness of surviving trees was probably associated with spatial variation in fire intensity, particularly with distance from pines. Initial fires acted as an "intermediate disturbance," maximizing spatial heterogeneity; whereas repeated fires and 1, 2, and 5-year intervals eventually left only a few isolated clumps. In contrast, 4-yr changes in an unburned reference field indicate that in the continued absence of fire, eventually trees thin and become more randomly distributed. Experimental approaches to studying pattern are extremely rare in the literature and completely absent among fire studies. Second moment spatial tests provided a powerful tool for examining pattern on a continuous scale. This flexibility was particularly important because the effects of fire on turkey oaks were highly scale-dependent, and a more traditional nearest neighbor index yielded inconsistent results. Although Monte Carlo tests were used to simulate random point distributions, tests could easily be developed to simulate hypothesized fire-removal processes, and thus slowly isolate the factors influencing forest pattern.

Sand live oaks form clonal groves which are resistant

to sandhill fires. Small trees suffered high crown mortality from initial sandhill fires, whereas large trees were lost very slowly from repeated fires at 1 and 2-yr intervals. Most variation in crown survival was explained by the dbh of sand live oaks, and not by location within a grove or grove size. Sand live oaks also suffered high crown mortality near longleaf pines, but mortality rates declined rapidly beyond 4-5 m from a pine. Groves recover from fire by resprouting, but lateral suckers are also produced annually as part of normal clonal growth and expansion.

Both turkey oaks and sand live oaks are very fire resistant with the capacity to persist under the extreme sandhill fire regime. With frequent and periodic fires, these oaks will slowly lose their dominance in sandhill, particularly near longleaf pines. However, their ability to persist vegetatively insures their regrowth during periods of infrequent fires.

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**Major Field:** Botany

**Title of Dissertation:** The effects of fire on forest community composition, structure, and pattern in Florida sandhills

**Approved:**

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